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Geological and Ichthyological Investigations into Palaeodrainage Hypothesis for the Tennessee River

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The University of Southern Mississippi

GEOLOGICAL AND ICHTHYOLOGICAL INVESTIGATIONS INTO PALAEODRAINAGE HYPOTHESES FOR THE TENNESSEE RIVER

by

Andrea Karen Persons

Abstract of a Dissertation
Submitted to the Graduate School
of the University of Southern Mississippi
in Partial Fulfillment of the Requirements
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ABSTRACT

GEOLOGICAL AND ICHTHYOLOGICAL INVESTIGATIONS INTO PALAEODRAINAGE HYPOTHESES FOR THE TENNESSEE RIVER

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The course of the ancestral Tennessee River has been debated in both the geological and biological literature for over 100 years. Several of the proposed courses for the ancestral Tennessee place its course across the state of Mississippi. Geochemical analysis of sedimentary rocks in the Pascagoula River basin supports these hypotheses suggesting that the rocks in the Pascagoula basin were derived from the Highland Rim of Tennessee and northern Alabama, while geochemical analysis of rocks from the Pearl River basin point to deposition from a mixture of sources including the ancestral Mississippi River and perhaps the ancestral Tennessee. To delve deeper into the history of the Tennessee River, the phylogenetic systematics of the *Etheostoma* subgenus *Doration* were used to further test these hypotheses. Results of the phylogenetic analyses suggest that the members of *Doration* along the Highland Rim are diverged from not only the remaining *Doration*, but also from one another due to the breaching of the Fort Payne chert atop the Nashville Dome during the Miocene. From the phylogenetic analyses, it is unclear whether the ancestral Tennessee crossed Mississippi, but a couple of patterns are evident. First, the results suggest that a stream capture event occurred between Bear Creek of the lower Tennessee drainage and one of the eastern tributaries to the Tombigbee River of the Mobile basin. Second, *Etheostoma stigmaeum* from the Pascagoula River basin are consistently recovered as monophyletic. When coupled with the geological evidence, these findings suggest that the history of Pascagoula River basin may be independent of its neighboring drainages on the coastal plain, possibly due to the mobilization of salt domes in the subsurface of the Gulf of Mexico coastal plain.

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LIST OF ABBREVIATIONS

A – Adenine

A – Arithmetic Mean

AKP – Field Notes of Andrea Karen Persons

Al – Aluminum

ANOSIM – Analysis of Similarity

B or (v) – Branch Length

BC – Bear Creek

Be – Beryllium

BP – Bayou Pierre

bp – Base Pair

BSPR – Blount Springs

C – Celsius

C – Cytosine

Ce – Cerium

CHVH – Central Highland Vicariance Hypothesis

CI – Consistency Index

cm – centimeter

cn – Chondrite Normalized

CS – Camp Shelby

Cyt *b* – Cytochrome *b* Gene

DNA – Deoxyribonucleic Acid

dNTP – Deoxynucleotide-Triphosphate

Eu – Europium

G – Geometric Mean

g – Gram

G – Guanine

GC – Grinders Creek

Gd – Gadolinium

GOM-CP – Gulf of Mexico Coastal Plain

HREE – Heavy Rare Earth Elements

I-D – Interdistributary

KYFWR – Kentucky Fish and Wildlife Resources

L – Likelihood

L – Tree Length

La – Lanthanum

LREE – Light Rare Earth Elements

LUX – Luxapalila Creek

M or (θ) – Model

MCMC – Markov Chain Monte Carlo

MDH – Mad Dog Hill

µg – Microgram

mm – Millimeters

mM – Millimole

ML – Maximum Likelihood

MMNS – Mississippi Museum of Natural Science

MORB – Mid-Oceanic Ridge Basalts

MPT – Most Parsimonious Tree

N – North

n – Normalized Concentration

NASC – North American Shale Composite

ND5 – NADH Subunit 5

P – Probability

PAAS – Post Archean Average Australian Shale

ppm – Parts Per Million

PCR – Polymerase Chain Reaction

PI – Parsimony Informative

Pr – Praseodymium

PSC – Phylogenetic Species Concept

REE – Rare Earth Elements

RI – Retention Index

SL – Standard Length

SLP – Field Notes of Steven Powers

Sm – Samarium

SRC – Standing Rock Creek

T – Thymine

T or (τ) – Topology

Taq – *Thermus aquaticus*

TBR – Tree Bi-Section Reconnection

TC – Topisaw Creek

Tenn-Tom – Tennessee-Tombigbee

TL – Total Length

TVA – Tennessee Valley Authority

U – Unit

UAIC – University of Alabama Ichthyology Collection

USM – University of Southern Mississippi

W – West

WTS – Field Notes of William T. Slack

Yb – Ytterbium

YFTC – Yale Fish Tissue Collection

CHAPTER I

PALAEODRAINAGE HYPOTHESES FOR THE TENNESSEE RIVER

Introduction

> Perhaps the best explanation for the strange course of the Tennessee River is that probably it is not a single river at all but rather is made up of three earlier rivers, stuck together like the parts of some Rube Goldberg contraption designed to move water from one place to another in the most unlikely way possible (Luther 1977).

That the modern course of the Tennessee River is anomalous is not disputed (e.g., Adams, 1928, Luther, 1977), but how it achieved this anomalous course is highly contentious. Beginning at the confluence of the Clinch and Holston Rivers, the Tennessee flows southwestward towards the Gulf of Mexico along the strike of the Valley and Ridge of the lower Appalachians until it reaches Guntersville, Alabama. There, instead of taking a direct path to the Gulf across Alabama, it makes a right angle and heads northwestward towards Mississippi, where it nicks the corner of the state and makes a second anomalous turn – this time to the north, cutting across the state of Tennessee until it confluences with the Ohio River in western Kentucky (Fig. 1).

Over the last 135 years, surveyors and geologists have proposed numerous hypotheses based on stratigraphy and structure to explain this anomaly (e.g., Long, 1875; Hayes and Campbell, 1894; White, 1904; Adams, 1928; Milici, 1968; Clark, 1989; Self, 2000; Mills and Kaye, 2001). Of especially contentious debate is whether or not the Tennessee River historically drained directly into the Gulf of Mexico. Most agree that the Tennessee probably had an outlet to the Gulf via the Mobile basin, but whether it was a direct connection remains unresolved (Long, 1875; Hayes and Campbell, 1894; White, 1904; Satterfield, 1961; Milici, 1968; Ross, 1971; Mills and Kaye, 2001; Mills et al. 2005).

Geologists are not alone in their curiosity about this potential former connection. Biologists, especially malacologists, such as Tryon (1873), Simpson (1900), van der Schalie (1938, 1939), and Matteson (1948) have noted the close relationships between the snails and mussels of the Tennessee River and the Coosa River of the Mobile Basin of Georgia and Alabama. More

recently, meristic studies and the genetic variation inferred from molecular systematic studies has recognized the Mobile basin as a hotspot of endemicity, especially among fishes, and these endemics are most closely related to species found in the Tennessee drainage (Table 1.1) (e.g., Ross, 1971; Swift et al., 1986; Etnier and Starnes, 1993; Wood, 1996; Boschung and Mayden, 2004).

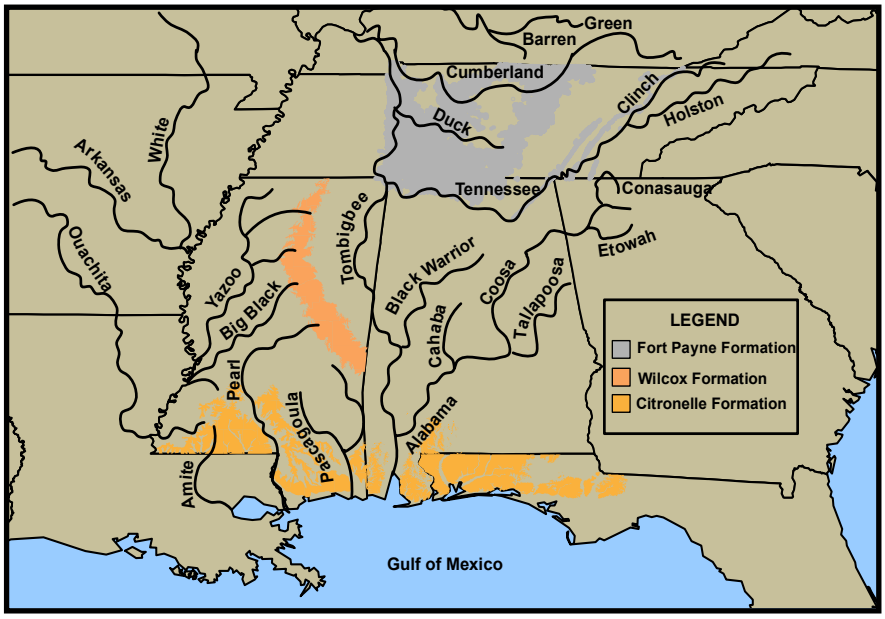

Fig. 1.1. Modern locales of selected drainages and geologic formations relevant to paleodrainage models for the Tennessee River. The locale of the Wilcox formation coincides with the sea-level maximum of the Eocene, and the locale of the Citronelle formation coincides with the sea level maximum of the late Miocene-Pliocene.

Johnson (1905, 1939) and Mills and Kaye (2001) considered this evidence circumstantial, but this taxonomic relationship is repeated and maintained across numerous taxa (Table 1.1), and, as advocated by Adams (1901) over 100 years ago, it needs to be considered as strongly as stratigraphy and structure in investigations of paleodrainage configurations of the Tennessee.

Table 1.1

Examples of Organisms that Provide Support for the Existence of a Connection between the Tennessee and Mobile Basins

Organisms	Author(s)	Basis of Support	Distribution
Snails			
Pleurocera	Tryon, 1873	Distributional Patterns	Tennessee, Ohio, & Alabama Drainages
Lithasia			Tennessee, Ohio, & Alabama Drainage
Goniobasis			Widespread incl. Tennessee & Mobile Basins
Anculosa			Tennessee, Ohio, and Coosa Drainages
Mussels[a]			
Medionidus conradicus	Simpson, 1900	Distributional Patterns &	Tennessee, Cumberland, & Ohio Drainages
Plethobasus cicatricosus		Taxonomic Relationships	Tennessee, Cumberland, & Ohio Drainages
Villosa iris			Widespread incl. Tennessee Drainage
Epioblasma brevidens	van der Schalie, 1938	Distributional Patterns &	Tennessee & Cumberland Drainages
Epioblasma metastriata		Taxonomic Relationships	Mobile Basin
Hamiota altilis			Eastern Mobile Basin
Lampsilis fasciola			Widesprad incl. Tennessee Basin
Lasmigona holstonia			Tennessee & Upper Coosa Basins
Medionidus conradicus			Tennessee & Cumberland Basins
Medionidus parvulus			Mobile Basin
Pleurobema decisum			Mobile Basin
Pleurobema oviforme			Tennessee & Cumberland Drainages
Ptychobranchus fasciolaris			Widespread incl Tennessee Basin
Ptychobranchus greenii			Tombigbee Drainage
Quadrula asperata			Coosa River
Quadrula keineriana			Alabama Drainage
Quadrula pustulosa			Widespread incl. Tennessee & Alabama Basins
Toxolasma corvunculus			Mobile Basin

Table 1.1 (continued).

Organisms	Author(s)	Basis of Support	Distribution
Toxolasma cylindrellus			Tennessee Basin
Utterbackia imbecillis			Widespread incl. Tennessee & Mobile Basins
Villosa iris			Widespread incl. Tennessee Drainage
Villosa vanuxemensis			Tennessee, Cumberland, & Upper Coosa Basins
Crayfishes[b]			
Cambarus extraneus	Adams, 1901	Distributional Patterns	Tennessee & Coosa-Alabama Drainages
Cambarus spinosus			Tennessee & Coosa-Alabama Drainages
Orconectes erichsonianus			Tennessee & Coosa-Alabama Drainages
Cambarus extraneus	Ortmann, 1905	Taxonomic Relationships	Tennessee & Alabama Drainages
Cambarus latimanus			Tennessee & Alabama Drainages
Orchonectes erichsonianus			Tennessee & Alabama Drainages
Fishes[c]			
Campostoma oligolepis	Ross, 1952	Taxonomic Relationships & Distributional Patterns	Widespread incl. Tennessee & Mobile Basins
Cottus carolinae	Wiley and Mayden, 1985	Distributional Patterns	Tennessee & Mobile Drainages
Lamptera aepyptera	Swift et al., 1986	Taxonomic Relationships & Distributional Patterns	Widespread incl. Tennessee & Mobile Basins
Acipenser fulvescens			Widespread incl. Tennessee & Coosa Drainages
Campostoma oligolepis			Widespread incl. Tennessee & Mobile Basins
Hemitrema flammea			Tennessee, Cumberland, & Coosa Drainages
Hybopsis lineapunctata			Coosa & Tallapoosa Drainages
Luxilus chrysocephalus			Widespread incl. Tennessee & Mobile Basins
Lythrurus lirus			Tennessee, Coosa, & Cahaba Drainages
Notropis chrosomus			Mobile Basin
Notropis stilbius			Mobile Basin

Table 1.1 (continued).

Organisms	Author(s)	Basis of Support	Distribution
Notropis xaenocephalus			Coosa, Tallapoosa, & Chattahootchee Drainages
Phenacobius catostomus			Mobile Basin
Rhinichthys atratulus			Widespread incl. Tennessee & Coosa Drainages
Hypentelium etowanum			Mobile Basin
Moxostoma duquesnei			Widespread incl. Tennessee & Mobile Basins
Moxostoma erythrurum			Widespread incl. Tennessee & Mobile Basins
Fundulus stellifer			Coosa-Alabama Drainage
Etheostoma coosae			Coosa Drainage
Etheostoma jordani			Coosa-Alabama Drainage
Etheostoma trisella			Coosa Drainage
Percina palmaris			Coosa & Tallapoosa Drainages
Etheostoma jordani	Wood, 1996	Phylogenetic Relationships	Coosa-Alabama Drainage
Etheostoma douglasi			Black Warrior Drainage
Etheostoma chuckwachatte			Tallapoosa Drainage
Etheostoma etowahae			Etowah Drainage
Etheostoma acuticeps			Nolichucky & Holston Drainages
Percina antesella	Near, 2002	Phylogenetic Relationships	Coosa-Alabama Drainage
Pecina tanasi			Tennessee Drainage
Hypentelium etowanum	Berendzen et al., 2003	Phylogenetic Relationships	Mobile Basin
Hypentelium nigricans			Widespread incl. Tennessee Drainage
Fundulus catenatus	Ghedotti et al., 2004	Phylogenetic Relationships	Widespread incl. Tennessee Drainage
Fundulus bifax			Coosa & Tallapoosa Drainages
Fundulus stellifer			Coosa-Alabama Drainages

Table 1.1 (continued).

Organisms	Author(s)	Basis of Support	Distribution
Salamanders			
Eurycea bisilineata	Kozak et al., 2006	Haplotype Divergence	Widespread incl. Tennessee & Mobile Basins
Turtles			
Sternotherus minor peltifer	Iverson, 1977	Distributional Pattern	Widespread incl. Tennessee & Mobile Basin

Note. a. Mussel taxonomy was updated from the original publications using Parmalee and Bogan (1998) and Williams et al. (2008).
b. Crayfish taxonomy was updated from the original publications through personal communication with C. B. Dillman (2010).
c. Fish taxonomy was updated from the original publications using Boschung and Mayden (2004).

Although most of the hypotheses proposing a connection between the Tennessee and Mobile basins predate both the plate tectonics and molecular biology revolutions, a connection between the two basins as proposed by these early studies may help explain the present-day distributions of closely related fishes in the two basins and could help explain these relationships (Table 1.1); however, recent hypotheses suggest that the ancestral Tennessee once connected to the Gulf of Mexico via a course across the state of Mississippi (e.g., Galloway 2005; Combellas-Bigott and Galloway, 2006), and these hypotheses remain untested by molecular phylogenetics. Stern (1976) has noted that such a course could explain the affinity of the unionid mussels found in the Lake Maurepas-Pontchartrain-Borgne drainage of southwestern Mississippi and Louisiana to those of the Coosa-Alabama system. Similarly, Fitzpatrick (1986) has argued that such a course could explain the present distribution of members of the crayfish family Cambaridae, but these hypotheses have not been rigorously tested as studies of the phylogenetic relationships among aquatic organisms in the drainage basins of Mississippi and studies concerning the provenance of Gulf Coastal Plain sediments in Mississippi are lacking. Several of these hypotheses will be examined in detail and then taken in context with modern knowledge of not only geology but also the geographic distributions of fishes.

Paleodrainage Hypotheses Connecting the Tennessee and Mobile Basins

Long (1875)

Long (1875), in his survey of the Holston and Tennessee Rivers, suggested that prior to its course through Walden Gorge, the Tennessee River once flowed directly into the Gulf of Mexico via the Coosa-Alabama River system. This suggestion was based on the geomorphology of Lookout Mountain and its adjacent valleys. Long (1875), noting the proximity, width, and the present sharing of these valleys by tributaries to both the Tennessee and Coosa Rivers believed that these valleys previously served as conduits for the Tennessee River to flow directly into the Gulf of Mexico.

Hayes and Campbell (1894) and Hayes (1899)

One of the first comprehensive studies of the anomalous course of the Tennessee was that of Hayes and Campbell (1894). Subsequently, the geomorphology of the area was reviewed by Hayes (1899), who reiterated many of the same concepts put forth in Hayes and Campbell (1894). As this hypothesis predates plate tectonics, it relies on the relict concept of geosynclines and the ability of subaerial erosion to erase the products of orogenesis. Hayes and Campbell (1894) believed that cycles of crustal flexure were tied to epeirogeny whereby transgressions (sea-level rise) caused depressions (valleys) while regressions (sea-level fall) left uplifts (mountains). In the southern Appalachians, the last major orogenic activity occurred during the Carboniferous (Hatcher et al., 1989); however, Hayes and Campbell (1894) and Hayes (1899) believed that there were subsequent uplift and baseleveling events, accompanied by crustal warping, especially during the Tertiary. This concept was as follows: (1) Major orogenesis in the southern Appalachians culminated in the late Paleozoic. (2) By the Cretaceous, the Cumberland base-leveling epoch closed with most of the late Paleozoic topography being erased by subaerial erosion resulting in a Cretaceous peneplain. At this time, drainages of the Cumberland Plateau were directed westward towards the Mississippi Embayment. (3) Epeirogeny ensued sometime in the early Tertiary resulting in uplift in the region of the Smoky Mountains, with the ridges of the Valley and Ridge being monadnocks, or high plateaus formed by fluvial erosion at their bases (valleys). This episode of fluvial erosion may be the Highland Rim epoch of Hayes (1899) which was loosely dated as Eocene. At this time, many of the westward flowing rivers were directed towards the south as a result of the uplift. (4) Following this episode, a final base-leveling event, the Coosa epoch, occurred sometime in the late Tertiary which culminated with a tributary to the Sequatchie River capturing the ancestral Tennessee which directed it through Walden Plateau establishing its present course (Figs. 1.2 and 1.3).

With respect to the Tennessee River, Hayes and Campbell (1894) argue that during the Cretaceous, the ancestral Sequatchie River flowed through the Sequatchie Valley and connected

to the Black Warrior River in Alabama. The Sequatchie River was captured when a stream flowing towards the Mississippi Embayment, occupying the same course as the modern Tennessee, headcut into the Sequatchie diverting it towards the embayment leaving the lower portion of Sequatchie valley unoccupied. An Appalachian River, which drained the southern Appalachians from the New/Kanawha basins of Virginia to the Cretaceous sea also existed at this time (Fig. 1.2).

Fig. 1.2. Approximation of the Cretaceous course of the ancestral Sequatchie and Appalachian Rivers of Hayes and Campbell (1894). Modified from Hayes and Campbell (1894) and Johnson (1905).

It had two branches that confluenced at the Coosa River in the vicinity of Rome, Georgia. The western branch flowed through the approximate routes of the present Clinch and Tennessee Rivers to Chattanooga, Tennessee, where it then continued towards Rome, Georgia via the Chickamauga and Chattooga Rivers. Flowing through the approximate course of the Holston River, the eastern branch flowed to Knoxville, Tennessee, and then followed the base of the Smoky Mountains until it reached its confluence with the western branch at Rome, Georgia.

This Appalachian River then continued down the Coosa and Alabama Rivers to the Gulf of Mexico depositing the Cretaceous and early Tertiary strata that now overlie central Alabama. Hayes and Campbell (1894) further argue that during the Tertiary, the pirated Sequatchie River flowed to the Mississippi Embayment by following the present course of the Big Black River across Mississippi, a hypothesis that has largely been overlooked. In the late Tertiary, as a depression formed from deposition of the "Lafayette" gravels, the western branch of the Appalachian River was diverted through Walden Gorge near Chattanooga, Tennessee when tributaries to the Sequatchie and Appalachian Rivers headcut through Walden Plateau from opposite sides creating Walden gorge, allowing for the capture of the Appalachian River turning it on its southwestward path through Alabama via the ancestral Sequatchie, where it then continued towards the Mississippi Embayment. This newly diverted stream was the ancestral Tennessee (Fig. 1.3). Hayes (1899) has placed the diversion of the western branch as occurring to the Coosa epoch of the late Tertiary. It was able to maintain this path because the Sequatchie River valley west of Chattanooga, Tennessee was at a lower elevation and was able to capture the newly diverted river (Figs. 1.4 A and B and 1.5).

Hayes and Campbell (1894) offered three features as support for the late Tertiary diversion process. First, it was argued that the divide between the Tennessee and Coosa is narrow and planed down from the Appalachian River flowing across it. Second, it was argued that the volume of Cretaceous and Tertiary sedimentation across central Alabama could be explained by the presence of the Appalachian River. Finally, it was argued that Walden gorge is too narrow to have been in existence for a substantial period of time. Following the diversion of the western branch of the Appalachian River through Walden gorge, another cycle of uplift ensued tilting the land towards the northwest. Many of the smaller streams were directed northwest into the Ohio drainage, but the ancestral Tennessee was able to maintain its path to the Mississippi Embayment via the Big Black River until one of the northwestward flowing streams headcut into the ancestral Tennessee in northeastern Mississippi setting the Tennessee on its modern course.

Problems with Hayes and Campbell (1894) and Hayes (1899)

The first major line of evidence that Hayes and Campbell (1894) cite for drainage reorganization lies in the nature of the divide between the Tennessee and Coosa Rivers. This divide is considered narrow and planed down as a result of the Appalachian River flowing across the divide and leveling it. Hayes and Campbell (1894) themselves admit that this evidence is problematic as similar divides, not attributed to a river flowing across them, are found elsewhere in the Appalachians. This point was reiterated by White (1904). Also problematic is the timing. Hayes and Campbell (1894) timed the diversion of the western branch as contemporaneous with deposition of the "Lafayette" gravels. Deposition of the "Lafayette" gravels is timed as Pliocene (Nelson et al. 2003), but Hayes and Campbell (1894) note that no channels are cut into the late Tertiary sediments of the Tennessee-Coosa divide. Hayes (1899) also reiterated this point, noting that the present courses of the Tennessee and Coosa Rivers had been established prior to the late Tertiary as no evidence of baseleveling occurs on the Tennessee-Coosa divide as a result of the Coosa epoch, which means that no baseleveling of the divide occurred during the late Tertiary. If no evidence of incision is found in *any* Tertiary sediments of the divide then two explanations are possible. The first is that a river never flowed across the divide. The alternative is that the diversion of such a river occurred much earlier. Adams (1928) has argued that the latter is true, and that the modern Tennessee River has maintained its present course since the Cretaceous and no piracy of an Appalachian River ever occurred. This view is supported by White (1904) and Johnson (1905). Ross (1971) has noted that it is possible that the Tennessee River has always maintained its course through Walden Gorge and that the faunal affinities observed between the Tennessee and Mobile basins may be due to small stream piracy events that occurred between the Hiwassee River, a tributary of the Tennessee River, and the Oostanaula River, a tributary to the Coosa River.

Fig. 1.3. Course of the Tertiary Tennessee River. Modified from Chamberlin and Salisbury (1905).

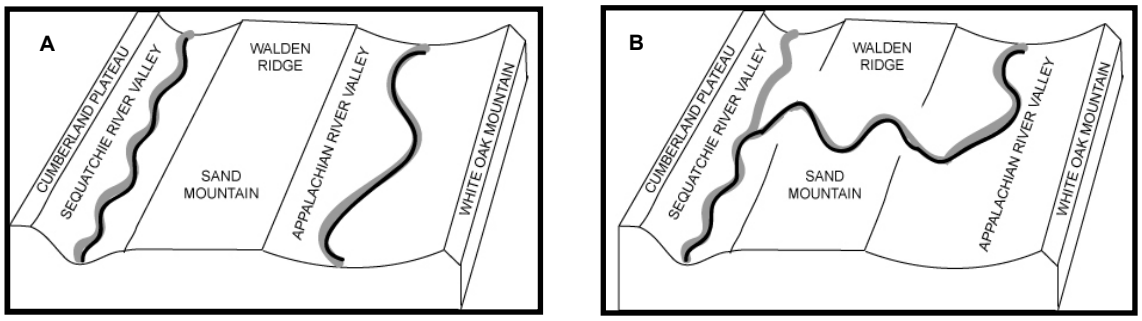

Fig. 1.4. A Cross-section showing the Cretaceous – early Tertiary course of the Appalachian River of Hayes and Campbell (1894). Fig. 1.4 B Cross-section showing the breaching of Walden Plateau and the subsequent piracy of the Appalachian River into the Sequatchie River valley creating the modern Tennessee. Modified from Johnson (1905).

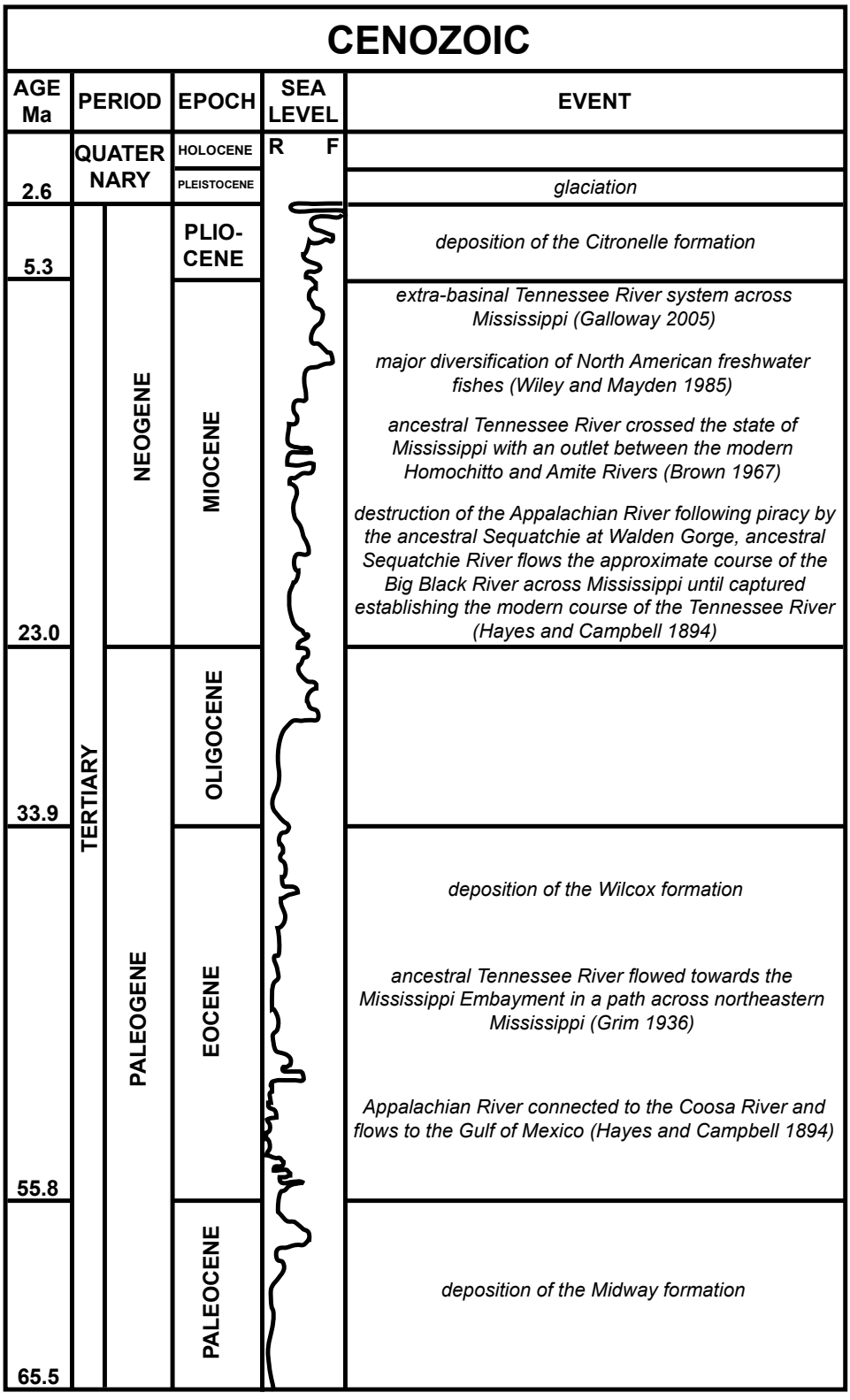

Fig. 1.5. Geological time scale charting sea level and the major palaeodrainage events of the Cenozoic. Time scale modified from Walker and Geissman (2009). Sea level curve modified from Haq et al. (1987).

Subsequent criticism of the hypothesis of Hayes and Campbell (1894) and Hayes (1899) was founded on the structural control exerted upon the course of a river. Hayes (1899) believed that crustal warping as a result of uplift was the most important factor influencing the geomorphology of fluvial systems. For example, the ridges of the Valley and Ridge could be formed by uplift, while the valleys could be formed by fluvial incision as a response to changes in baselevel, but White (1904) pointed out that features such as the Valley and Ridge did not require fluvial incision to form, and that these features were a result of structure. White (1904) further argued that the second line of evidence, the amount of sediments deposited in central Alabama, could not solely be attributed to the deposition of eroded materials by the Appalachian River, as the Cretaceous deposits were marine in origin. Also, White (1904) noted that no evidence suggested that the Coosa-Alabama system was ever any larger than at present and could not be considered a route for transportation of all of the eroded materials deposited in central Alabama. Noting that the thickness of the lignitic beds deposited in central Alabama were less than that of those deposited in western Alabama and eastern Mississippi, White (1904) argued that some of the central Alabama sedimentation could be attributed to transportation from the west. Finally, White (1904) discussed the narrow size of Walden Gorge and pointed out that similar narrow gorges are found in the older upper Tennessee valley, indicating that piracy of an Appalachian River through Walden Gorge was unlikely suggesting that the modern courses of the Tennessee and Coosa rivers could not have been altered in the manner envisioned by Hayes and Campbell (1894). Johnson (1905) concurred, noting that the winding pattern of the Tennessee River through Walden Plateau would have taken an amount of time greater than the Tertiary to establish itself, indicating the present course of the Tennessee had been established since the Cretaceous.

It is now understood that structural features such as the Valley and Ridge were formed by thrust-folding processes initiated by the continental-continental collision of Laurentia and Gondwana during the Alleghany Orogeny (Hatcher et al., 1989) and not by fluvial incision; thus, the Valley and Ridge is a long-standing topographical feature of the Southern Appalachians, and

if a river incised one of the valleys, evidence of such a recent event should remain. Further, Cretaceous formations such as the Ripley were not deposited as a result of the erosion of carbonaceous sediments by a fluvial system such as the western branch of the Appalachian River as suggested by Hayes and Campbell (1894). Instead, as White (1904) recognized, the Cretaceous deposits of the Gulf Coastal plain are marine deposits.

In addition to these criticisms, Shaw (1918) noted that many of the details surrounding the history of the Tennessee River as outlined by Hayes and Campbell (1894) needed modification, and further argued that the Tennessee River never utilized the Big Black River in a course towards the Mississippi Embayment. Shaw (1918) based his argument on the lack of high terraces along the Big Black River and the lack of an abandoned river valley between the Big Black and the Tennessee River systems. Based on the same evidence, Shaw (1918) further argued that it was improbable that the Tennessee ever utilized the Yalobusha, Yocona, or Tallahatchie River systems, whose valleys are proximal to that of the Big Black River.

Hayes (1899) noted that the correlation between the geomorphology and drainage configuration of the Appalachian River was the result of complex processes which were subject to unknown factors, and the conclusions of geomorphic assessments of the area should be considered with caution, and that further studies, especially with respect to the recent geological history of the area, were needed.

Satterfield (1961)

Satterfield (1961) examined possible connections between the rivers of southeastern Tennessee, Alabama, and northern Georgia using fishes, and noted that for a natural expansion of fishes between adjacent drainages, a connected watercourse is needed. Recognizing the high level of fish endemicity within the Tennessee and Mobile basins, Satterfield (1961) argued that the basins were old, large enough to provide a variety of habitats, and were geographically isolated for extended periods of time. Species may have moved between the drainages or dispersed from a common source to the different drainages. Further, Satterfield (1961) noted that

it may be possible that the Alabama River system is a remnant of an old, now abandoned course of the Tennessee, but piracy between the two systems especially in the vicinity of the Valley and Ridge seems unlikely due to the entrenched nature of the Coosa River. Instead, Satterfield (1961) attributed the faunal similarities between the basins to stream piracy events in the vicinity of the Etowah River basin. Satterfield (1961) also noted that the distributions of species in the percid fishes genera of *Etheostoma* and *Percina* provide strong evidence for a former drainage connection between the Tennessee and Mobile basins, as they are found extensively throughout these basins, but are absent from adjacent streams such as the Chattahoochee in Georgia.

Wall 1968

Based on comparisons of scale counts of the percid fish *Etheostoma stigmaeum* and the cyprinid fish *Notropis baileyi* found in Bear Creek, a tributary to the Tennessee River, to those found in the Tombigbee River, Wall (1968) hypothesized that the species found in the Tennessee River drainage were most closely allied to those found in the Tombigbee River. Wall (1968) believed that these two fishes, and perhaps others, entered the Bear Creek system from the Tombigbee River as a result of stream capture. The stream capture was believed to have occurred between tributaries to the Bear Creek system and tributaries to the Buttahatchee River, a direct tributary to the Tombigbee River, as a result of a surface tilting event which allowed the tributaries of the Buttahatchee River to headcut into those of Bear Creek.

Additional Paleodrainage Hypotheses

Mills and Kaye (2001) note that research regarding the historical course of the Tennessee River is lacking, and that most studies mention it only in passing; however there have been a few brief additional hypotheses put forth:

1. White (1904) hypothesized the presence of a Cretaceous trans-Appalachian River whose southern flowing branches rapidly headcut across the Cumberland Plateau capturing originally northwestward flowing streams such as the Nolichucky, French Broad, and Hiwassee redirecting them into the Tennessee River which then turned west and flowed

across the Walden plateau, implying that the modern course of the Tennessee was established in the Cretaceous, which is prior to the late Tertiary date assigned by Hayes and Campbell (1894); however, this hypothesis also relies on the baseleveling of the Appalachian Mountains with subsequent uplift events.

2. Based on the location and sorting of gravels in southern Tennessee, northwestern Alabama, and northeastern Mississippi, Kaye (1974) hypothesized that glacial meltwater coupled with an obstruction at the mouth of the Tennessee River led to spillover events that crossed drainage divides and flooded portions of Tennessee, Alabama, and Mississippi that are adjacent to the Tennessee River.
3. The presence of Blue Ridge derived "metaquartzite" clast bearing deposits along the western edge of the Tombigbee River suggests that the Tennessee River once utilized the old (unaltered) reach of the Tombigbee River in Mississippi (Mills and Kaye, 2001).
4. A transition from quartz to chert dominated gravels in the exposed Tennessee River terraces at Pickwick, Tennessee and a lack of chert in the gravels of the Hatchie River suggest that the Tennessee River flowed through the Hatchie River valley until the Fort Payne chert bearing Nashville Dome was breached in the Miocene-Early Pliocene (Self, 2000).
5. The stratigraphy and geomorphology of the upland river basins of Alabama and the taxonomic relationships of their riverine faunas suggest that the Tennessee River once flowed into the Black Warrior basin of Alabama and then continued this course into Mississippi (Rindsberg, 2002).
6. Based on the presence of an old alluvial band that crosses the Tennessee-Gulf of Mexico divide between the Ocoee and Conasauga Rivers, Mills et al. (2005) suggested that either the Conasauga River, which is presently a tributary to the Coosa River, was once a tributary to the Tennessee River or that the Ocoee River, which is presently a tributary to the Tennessee River, was once a tributary to the Coosa River.

As with previous hypotheses, these too are of contentious debate among geologists. These hypotheses are often difficult to access as they are found in meeting abstracts, while papers in peer-reviewed journals are lacking. There is no strong support either for or against the hypotheses (Adams, 1928; Mills and Kaye, 2001). The glacial dam hypothesis has come under scrutiny because it does not support the function of glacial mechanics related to bedrock removal (McSaveney, 1974). Also, the terrace deposits of the Tombigbee River at Columbus, Mississippi do not correlate well with those of the Tennessee River making a direct connection highly unlikely (Russell and Schmitz, 2003).

All of the hypotheses set forth are difficult to accept or discredit due to a lack of stratigraphical evidence, problems constraining the timing of the deposits, and the probability that all of the hypotheses could be correct given that, throughout its history, the Tennessee River could have directly connected to the Gulf of Mexico at multiple localities at either the same or multiple points in time. The hypothesis of Hayes and Campbell (1894) certainly seems outdated with the recognition of plate tectonics, but interestingly, although these hypothesized connections predate plate tectonics by ~70 years, the localities of their hypothesized connections would explain the close relationships between aquatic organisms in the Tennessee River basin to those of the Coosa River basin and are still under discussion. Taking into account previous geomorphic research, current geologic research, and the distributions of percid fishes, the hypotheses of Hayes and Campbell (1894) will be re-evaluated.

Could Hayes and Campbell (1894) and Hayes (1899) Have Been Right?

As already mentioned, Hayes and Campbell (1894) and Hayes (1899) note the lack of Tertiary or Quaternary incision across the divide between the Tennessee and Coosa Rivers. Also, as noted by Satterfield (1961), the Coosa is deeply entrenched into the Valley and Ridge. Hayes and Campbell (1894) have placed the age of the Coosa within the Cretaceous and have argued that progressive headward cutting of the Coosa resulted in the Valley and Ridge topography. It is today, however, understood that the Valley and Ridge certainly predates the Coosa River

(Hatcher et al., 1989). The deep entrenchment of the Coosa does suggest that it has maintained its course for a length of time, but the length of this time is difficult to assess. It would be expected that any form of fluvial incision across the strike of the Valley and Ridge, i.e. between the Tennessee and Coosa Rivers, would be recorded in its topography. An Appalachian River, therefore, seems unlikely; however, the hypothesis of Hayes and Campbell (1894) which suggests that the ancestral Sequatchie and Black Warrior Rivers were connected via the Sequatchie Valley has gained support.

Potential Connection via the Sequatchie Valley

Locality

The Sequatchie Valley of the Cumberland Plateau maintains a northeast to southwest trend through Tennessee and Alabama (Milici, 1960; Hatcher et al., 1989). It is flanked to the west by the Nashville Dome, and to the east, it is flanked by the Valley and Ridge (Fig 1.6). Flowing through the northern part of the valley is the Sequatchie River. Its course towards the Gulf of Mexico is interrupted by the Tennessee River, but the valley proper continues to the southwest into Alabama until it terminates at the Plateau-Valley and Ridge Boundary (Hatcher et al., 1989) near the Cahaba River at Birmingham, Alabama.

Structural Synthesis

The Sequatchie Valley consists of the Sequatchie anticline and the Sequatchie Valley fault. Analogous to the Pine Mountain thrust sheet, the Sequatchie anticline is a northwest-verging ramp anticline (Hatcher et al., 1989), which trends with the valley from Tennessee into central Alabama. At its northern end, the anticline links the Cambrian Rome formation to Pennsylvanian clastics (Hatcher et al., 1989). Cutting the anticline, and exposed on the northwest limb of the anticline, is the Sequatchie Valley Fault. Fault displacement decreases southward until it completely disappears in Alabama (Hatcher et al., 1989).

As a whole, the Cumberland Plateau, which contains Sequatchie Valley, is underlain by severely deformed Paleozoic rocks with the oldest units exposed at the surface (Milici, 1960;

1968). Milici (1968) argued that the joints in these deformed Paleozoic rocks may have controlled the path of the ancestral Tennessee especially from Chattanooga, Tennessee to the Sequatchie Valley. Milici (1968) further argues that the ancestral Tennessee was trapped by the Sequatchie anticline where it eroded through a Pennsylvanian caprock. Similarly, Miller (1990) has noted that during the Paleozoic, the area that is now the Sequatchie Valley was underlain by flat-lying limestone. The limestone was overlain by shale and sandstone. Onset of the Alleghany Orogeny increased folding in the area, and the limestone-sandstone sequence was fractured. Water was able to flow along the fracture, removing the sandstone caprock. The headcutting of the stream increasingly exposed the limestone until sinkholes developed near the beginning of the stream. The exposure is now the Sequatchie Valley (Miller, 1990).

Although Hayes and Campbell (1894) argue that a Cretaceous piracy event led to the formation of Sequatchie Valley, the timing of valley formation is not constrained. For the valley to trend into central Alabama, these fluvial processes would need to continue into Alabama. The Sequatchie River flows through the north part of the valley until it is cut by the modern course of the Tennessee River, leading to the question of what happened to southern portion of the river that extended the valley trend into central Alabama, and when did this beheading event occur?

Faunal Distributions

The Mobile basin of Alabama is home to many endemic species of freshwater fishes. Many of the closest relatives of the endemics are found within the Tennessee drainage (Table 1.1) (Wiley and Mayden, 1985; Swift et al., 1986; Mayden, 1988; Etnier and Starnes, 1993; Wood, 1996; Berendzen et al., 2003; Boschung and Mayden, 2004; Near and Keck, 2005). This information has largely been overlooked by geologists, but may provide tangible evidence as to where a former connection could have occurred.

Exemplary of the relationship between the Tennessee and Mobile basins is the darter (*Etheostoma*) subgenus *Nothonotus*. Four species of *Nothonotus* comprising the *Etheostoma jordani* species group are endemic to the Mobile basin. *Etheostoma jordani* is widely distributed

throughout the Upper Alabama, Cahaba, Coosa, and Tallapoosa Rivers, while *Etheostoma douglasi* is restricted to the Black Warrior River system, *Etheostoma chuckwachatte* is found only in the Tallapoosa River, and *Etheostoma etowahae* is restricted to the Etowah River (Wood and Mayden, 1993).

Based on the distributions of the species group, several lines of evidence are available in support of a former connection between the Tennessee and Mobile basins via the Sequatchie Valley. First, populations of *Etheostoma douglasi* are separated by the Sequatchie Fault. Second, at the termination of the valley near Birmingham, Alabama, numerous *Etheostoma jordani* populations can be found. Lastly, populations of *Etheostoma chuckwachatte* and *Etheostoma etowahae* are patchy indicating that they may have reached their present distributions recently, which would not be possible via the Appalachian River proposed by Hayes and Campbell (1894). The closest relative to the *Etheostoma jordani* species group is *Etheostoma acuticeps*, an endemic of the Nolichucky and Holston Rivers of Tennessee (Etnier and Starnes, 1993).

Once again, constraining the age of speciation among this group is difficult. Wiley and Mayden (1985) note that the speciation events of freshwater fishes occurred in drainage configurations different from those of today, and argue that these events predate the Pleistocene. Topographically, the appearance of a "fishhook" pattern on maps of the Tennessee River at Guntersville, Alabama, which sits in Sequatchie Valley, suggests that a stream piracy event occurred at this location at some point in time. It is possible that the ancestral Tennessee River connected to the Mobile basin via the Sequatchie Fault during the Paleocene and Eocene when sea level was higher and the marine Midway and Wilcox formations were deposited (Table 1.1). Tributaries to the Sequatchie Valley system may have included streams from the Coosa and Tallapoosa River basins which allowed the ancestral stocks of aquatic organisms to disperse between the basins. As sea level began to drop, drainages such as the Coosa were able to extend across the coastal plain and eventually connect to drainages that developed across the coastal plain as sea level continued to drop throughout the Miocene to Pleistocene epochs.

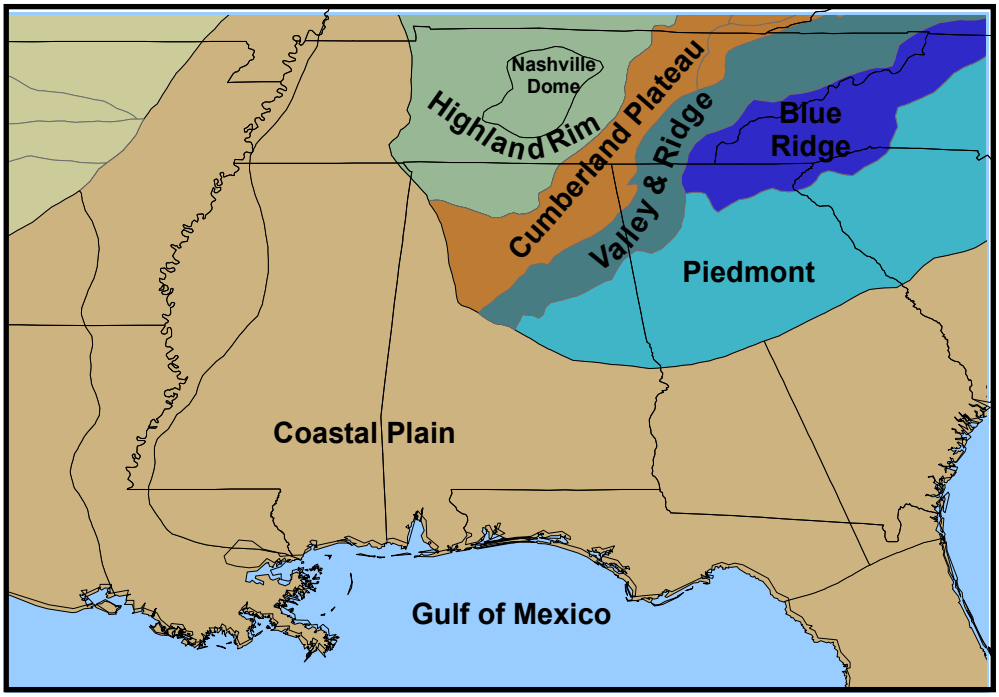

Fig. 1.6. Locales of physiographic regions mentioned in palaeodrainage hypotheses.

Contemporaneously, the Tennessee River assumed its modern course, separating its fauna from that of the Mobile basin allowing the separate faunas to differentiate. Further, events tied to glaciers may have contributed to further re-organization of the drainages (Wiley and Mayden, 1985). Cycles of base-level alteration leading to rapid incision followed by stability during the Pleistocene are preserved in cave sediments (Anthony and Granger, 2006), but how these events are tied to the evolution of Sequatchie Valley is unknown.

Hypotheses Placing the Course of the Ancestral Tennessee across Mississippi

Grim (1936)

Grim (1936) agreed with Hayes and Campbell (1894) that the ancestral Tennessee flowed through northeastern Mississippi towards the Mississippi Embayment during the early to mid-Eocene (Figs. 1.5 and 1.7). This hypothesis was based on the petrographic and mineralogical similarities between the sediments of the Midway and Wilcox formations of the Mississippi

Embayment to those of the southern Appalachians. Further, the Midway and Wilcox sediments were interpreted as being deposited in a delta that was formed at the mouth of the ancestral Tennessee. Grim (1936) believed that as the deposition of the Wilcox ended, and that of the Claiborne formation began, the ancestral Tennessee was diverted to its modern path.

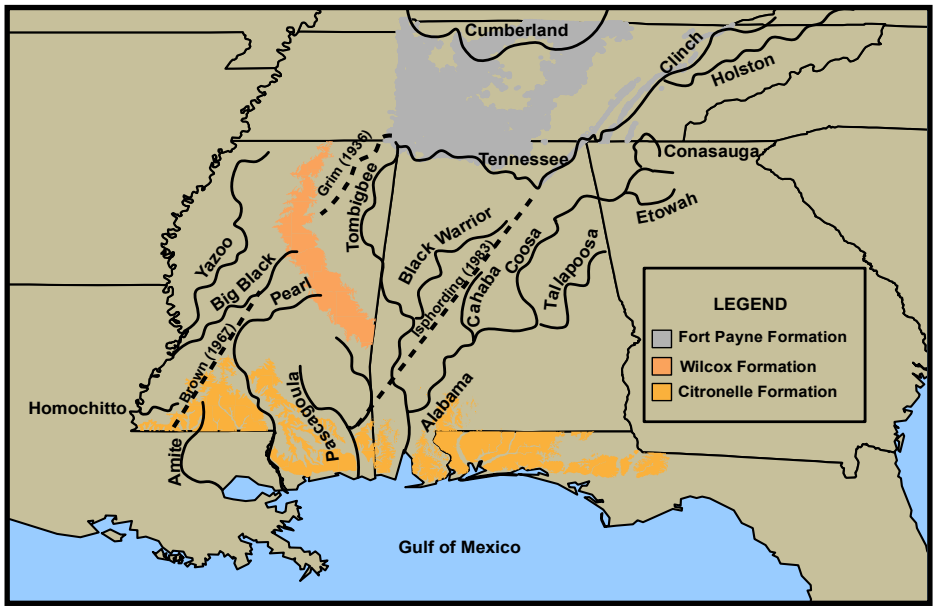

Fig. 1.7. Course of the ancestral Tennessee based on Grim (1936), Brown (1967) and Isphording (1983).

Brown (1967)

Brown (1967) also hypothesized that the ancestral Tennessee crossed Mississippi, trending from the northeast corner of the state to the southwestern corner of the state with an outlet between the modern Homochitto and Amite Rivers, but Brown (1967) believed that this course persisted past the Eocene until the Miocene or early Pliocene (Figs. 1.5 and 1.7). Evidence for this course included the textures and placements of fluvial deposits within the state. It was further hypothesized that the gravel deposits of the Citronelle formation were part of the ancestral stream bed. Brown (1967) also noted that many of the topographic anomalies of Mississippi could be explained by the ancestral Tennessee crossing Mississippi, and this aspect should be examined in more detail.

Isphording (1983)

Isphording (1983) examined mineral suites of the Miocene Hattiesburg clay formation taken from a salt dome near New Augusta, Mississippi in the Pascagoula River basin. The suite of minerals included the metamorphic minerals hornblende, epidote, and garnet. Mineral analyses from adjacent portions of the Hattiesburg clay lacked these metamorphic minerals, leading Isphording (1983) to conclude that these minerals were transported to the salt dome from the heavily metamorphosed Appalachian Piedmont via the ancestral Tennessee River. Isphording (1983) hypothesized that prior to its right-angle turn at Guntersville, Alabama, the ancestral Tennessee River continued in a southwestern trend across Alabama and Mississippi (Fig. 1.7). The Tennessee was turned on its modern course in response to uplift as a result of eustatic changes coupled with additional tectonic activity along the Gulf of Mexico margin. Subsequently, the Tombigbee and Alabama River systems developed in response to the tectonic activity (Isphording, 1983).

Extra-Basinal Tennessee River System across Mississippi

Recent work suggests that during the Miocene, extra-basinal fluvial systems existed across the coastal plains of Texas and Mississippi that were necessary to drain areas of rejuvenated isostatic uplift (Galloway et al., 1991; Boettcher and Milliken, 1994; Combellas-Bigott and Galloway, 2002; Combellas-Bigott and Galloway, 2006). Combellas-Bigott and Galloway (2002; 2006) believe that the extra-basinal system that crossed the coastal plain of Mississippi was the ancestral Tennessee River as suggested by Grim (1936) and Brown (1967) (Fig. 1.8).

During the early Cenozoic, the Nashville Dome was slowly eroding, an event which is contemporaneous with the Highland Rim epoch of Hayes (1899). Erosion accelerated during the Miocene when the Fort Payne chert (Mississippian) atop the Nashville Dome was breached leading to rapid downcutting and dissolution of the Cumberland Plateau (Luther, 1977; Stearns and Reesman, 1986; Reesman and Stearns, 1989; Galloway, 2005). During the Eocene and Miocene, climate changes coupled with the re-activated uplift of the Appalachians and localized

isostatic adjustment of the Nashville Dome initiated the extra-basinal ancestral Tennessee River system that transported sediment shed from the eroding Nashville Dome and southern Appalachians (Todd and Folk, 1957; Reesman and Stearns, 1989; Boettcher and Milliken, 1994; Xinxia and Galloway, 2002; Combellas-Bigott and Galloway 2002, 2006; Westaway 2007). The ancestral Tennessee was able to remove sediment from alluvial fans along the flanks of the dome and from the southern Appalachians and deposit it from offshore Louisiana to Alabama (Saucier, 1994; Combellas-Bigott and Galloway, 2002; Galloway, 2005; Combellas-Bigott and Galloway, 2006). This extra-basinal system most likely persisted until the Pleistocene (Galloway, 2005; Combellas-Bigott and Galloway, 2006).

The erosion of the Nashville Dome and the initiation of an extra-basinal fluvial system may explain the distribution of endemic species in the central basin and around the dome in Tennessee and northern Alabama. For example, Powers and Mayden (2007) described *Etheostoma planasaxatile*, which is found on the southwestern edge of the dome, *Etheostoma orientale*, which occurs on the northeastern flanks of the dome, and *Etheostoma tennesseensis*, which is found on the southern and eastern edges of the dome. It is likely that these species had a common ancestor that occurred in the area, but reorganization of tributaries by the extra-basinal system and the erosional bedload in these systems allowed differentiation of the ancestral stock to occur; however, the influence of the ancestral Tennessee on the modern courses of the Gulf coastal plain drainages is unclear. It is possible that the Amite, Pearl, and Pascagoula drainages of the coastal plain were formed as part of an interdistributary (I-D) bay complex that fanned out across the delta of the ancestral Tennessee helping to distribute the Citronelle deposits across Mississippi and Louisiana. As sea-level dropped in the Pleistocene, these I-D bay drainages could have persisted extending themselves across the shelf creating their modern geomorphology. Saucier (1994) argues that the lower ancestral Tennessee was probably pirated by the Mississippi River during a period of deepening. The mapping of Cenozoic sediments for hydrocarbon recovery, however, has shown that Tertiary growth faults underneath the gulf coastal plain are ubiquitous

(Nehring, 1991; Salvador, 1991). These growth faults could have broken and redirected the lower course of the ancestral Tennessee leading to the formation of the modern courses of the Pearl and Pascagoula Rivers.

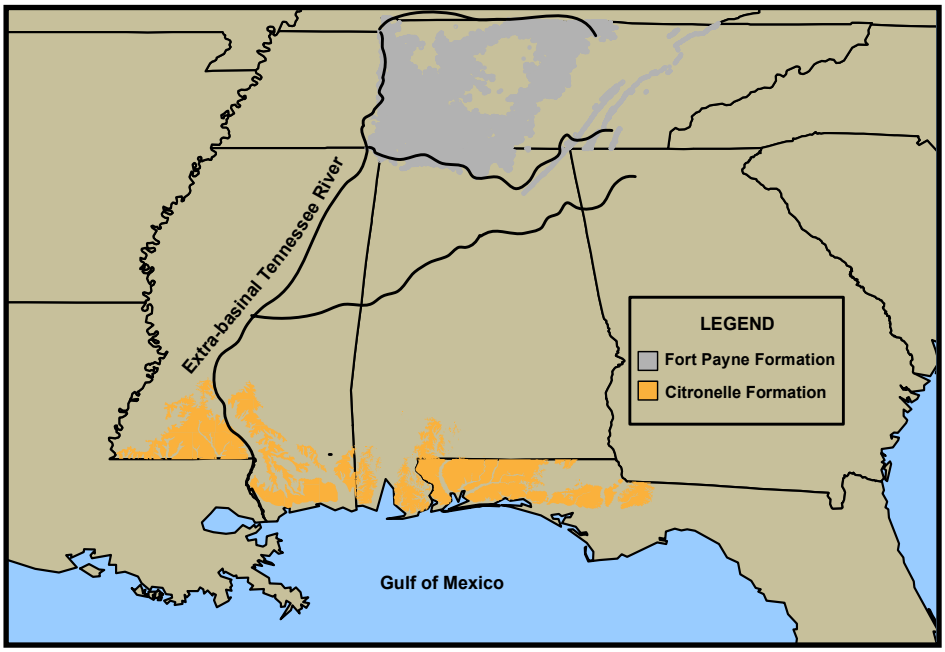

Fig. 1.8. Extra-basinal Tennessee River system. Modified from Galloway (2005) and Combellas-Bigott and Galloway (2006).

To reiterate, the modern course of the Tennessee River is still not well understood. At Guntersville, Alabama, the modern Tennessee turns at a right angle flowing into the northeastern corner of Mississippi. From Mississippi, it turns again at a right angle, flowing north across Tennessee until its confluence with the Ohio River. Sediment ages obtained from Al^{26} Be^{10} cosmogenic radionuclide dating along the Cumberland River have shown that during the Pliocene and Pleistocene, rivers of the Cumberland Plateau were subjected to cycles of increased baseflow and rapid incision, which were followed by periods of relative stability (Anthony and Granger, 2006). At approximately the same time, neotectonic activity was occurring along the Mississippi Embayment which subsequently led to the shifting of drainage basin axes (Garrote et al., 2006).

It is possible that the structural influence exerted by the Nashville dome and fault reactivation along a line from Guntersville, Alabama to northeastern Mississippi coupled with increased baseflow and incision pirated the course of the ancestral Tennessee to its modern course which concomitantly set the courses of the modern Black Warrior, Tombigbee, Big Black and Yazoo River systems.

Synthesis of the Drainage Hypotheses

In summary, geologic data and faunal distributions suggest that the ancestral Tennessee had two branches. The eastern branch flowed from Virginia, east of the Nashville Dome, to Guntersville, Alabama, and then continued into Alabama through the Sequatchie Valley. The western branch represents the diverted western branch of Hayes and Campbell (1894) and the extra-basinal fluvial system of Combellas-Bigot and Galloway (2006). This branch transported eroded material from the Nashville Dome to the coastal plain via a course across Mississippi. The eroded material was deposited in the Plio-Pleistocene age Citronelle formation. Following the deposition of the Citronelle, seismic activity along the Mississippi Embayment reorganized the axes of the drainage basins of Tennessee, northern Alabama, and northern Mississippi turning the Tennessee to its modern course.

Conclusions

Why the Tennessee River makes its anomalous turns is unknown. Several hypotheses have been proposed, most of which are of contentious debate. Many of the hypotheses predate plate tectonics, but the areas of the proposed former courses still seem feasible. Although geologists have written off biological evidence as circumstantial, it should not be overlooked. The Tennessee and Mobile Basins have repeated patterns of phylogenetic relationships across numerous taxa (Table 1.1). As it is a repeated pattern, it provides strong evidence of a former connection between the two basins; however, based on geological evidence, it seems unlikely that a direct connection between the Tennessee and Coosa Rivers ever existed. It seems more likely that tributary switching between the Tennessee and Coosa Rivers , as suggested by Long (1875),

Satterfield (1961), Ross (1971) and Mills et al. (2005), has occurred allowing the taxa found in one basin to shift to the other. Also, it is possible that the extension of the Sequatchie River into Alabama via Sequatchie Valley facilitated the movement of some species between the Tennessee and Mobile basins. The topography and gravel deposits of Mississippi also suggest the potential that the course of the ancestral Tennessee once flowed across the state. It should be reiterated, however, that it is possible that the ancestral Tennessee River had numerous outlets to the Gulf of Mexico, and these outlets may have occurred simultaneously or at different points during geological time. The events that led to modern courses of the systems under investigation are most likely due to a delicate interplay between the structural exertion of the Nashville Dome and palaeoseismicity along the Mississippi Embayment, but these hypotheses cannot be directly addressed until the phylogenetic relationships among aquatic organisms on the Gulf coastal plain are better understood, and until the provenance of the Gulf coastal plain deposits are further investigated.

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CHAPTER II

GEOLOGICAL INVESTIGATIONS INTO PALAEODRAINAGE HYPOTHESES FOR THE TENNESSEE RIVER: USE OF RARE EARTH ELEMENTS TO ASSESS THE ORIGIN OF THE CITRONELLE GRAVELS IN MISSISSIPPI

Introduction

Within the state of Mississippi, the three economically important gravel deposits that overlie portions the coastal plain are the Cretaceous Tuscaloosa Formation in the northeastern corner of the state, the Plio-Pleistocene Citronelle Formation in the southern part of the state, and the pre-loess/alluvial gravels that flank the eastern side of the Mississippi River (Fig. 2.1) (Russell, 1987). Due to their similarities, early geologic surveys of the state linked each of these deposits together (Hilgard, 1860), but subsequent surveys differentiated the deposits (Smith and Johnson, 1887; Matson, 1916; Fisk, 1938). The fluvial Tuscaloosa Formation gravels are disconformably overlain by the marine transgressive McShan and Eutaw Formations making them distinguishable from the Citronelle and alluvial gravels of the Mississippi River (Sohl et al., 1991); however, due to their similarities and a lack of diagnostic fossils, stratigraphic evaluation and differentiation of Citronelle deposits from both the alluvial floodplain gravels and from adjacent underlying strata along the Gulf of Mexico coastal plain (GOM-CP) is difficult (Matson, 1916; Fisk, 1938; Isphording and Lamb, 1971; Isphording, 1976; May, 1980). With outcrops along the coastal plain from Texas to Georgia, the Citronelle outcrops extensively in southern Mississippi, and is the most widespread of all coastal plain deposits (Doering, 1958; Otvos, 1998, 2004), but due to these problems, its age, provenance, and depositional history have been the subject of debate for more than a century.

The type locality of the Citronelle is located near Citronelle, Mobile County, Alabama where it was characterized by Matson (1916) as a mainly fluvial terrace deposit with some estuarine and re-worked strand line influences. Matson (1916) assigned it a Pliocene age based on fossil plants described from the formation by Berry (1916). The course and the age of the fluvial system(s)

that deposited the gravels and sands of the Citronelle remains unclear. Recently, Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005) hypothesized that from the Miocene to the Pleistocene, the ancestral Tennessee River acted as an extra-basinal fluvial system that flowed across the state of Mississippi and emptied into the GOM via the lower Pearl River basin (Fig. 2.2). The extra-basinal ancestral Tennessee was initiated in response to climatic changes, rejuvenated tectonic activity in the southern Appalachians, and localized isostatic adjustment of the Nashville Dome, and was responsible for the deposition of fluvial deposits along the GOM-CP (Reesman and Stearns, 1989; Boettcher and Milliken, 1994; Combellas-Bigott and Galloway, 2002; Galloway, 2005; Combellas-Bigott and Galloway, 2006).

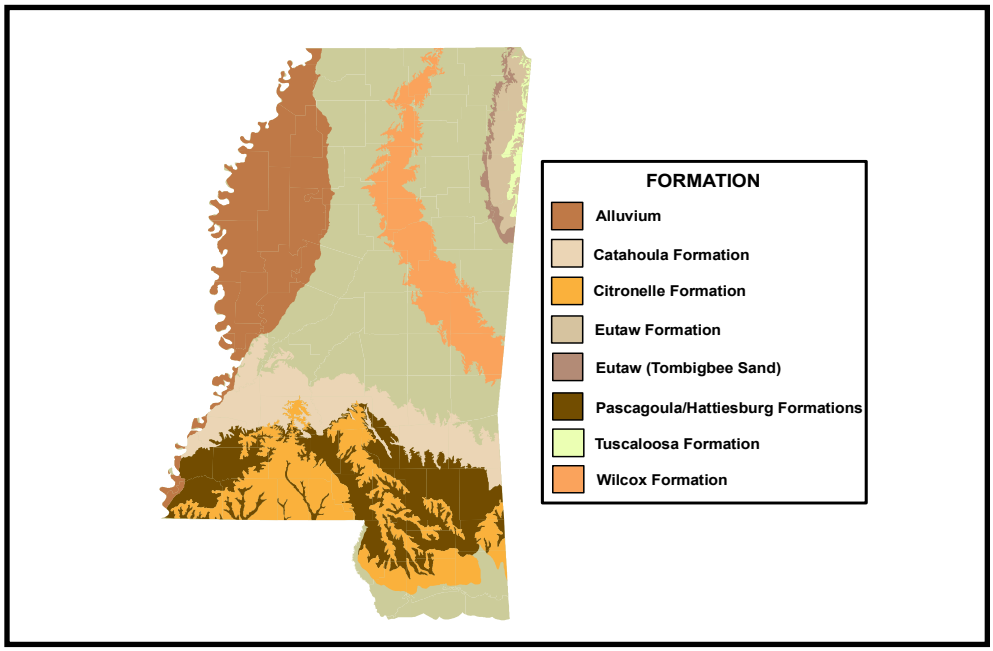


Fig. 2.1. Generalized geological map of Mississippi outlining the Formations relevant to this study.

These hypotheses are supported by the work of Cotten (1986) who mapped ten total terraces on the lower Pearl River in Mississippi. The first six terraces were identified as fluvial in nature, and the remaining four terraces were identified as former valley walls. Terrace one was equated to the modern floodplain and sits approximately 20 – 30 feet above the surface of the Pearl River.

With each subsequent terrace, the height above the surface of the modern river increases to a maximum of 160 feet on the sixth terrace. The tenth terrace, which delineates the Pearl River valley divide, sits at an elevation of 280 – 320 feet above the surface of the modern Pearl. Terrace five was identified as a paired terrace, which form when each terrace on both sides of the river is at the same elevation, and both are the result of the same downcutting event. This finding led Cotten (1986) to conclude that terrace five formed as a result of a rapid downcutting event in response to sea level or climate change, uplift, or a combination thereof, and, based on crustal warping rates, this downcutting event occurred ~1.9 MYA at the Pliocene/Pleistocene boundary, which fits with the timing of the extra-basinal system proposed by Combellas-Bigott and Galloway (2002), Galloway (2005), and Combellas-Bigott and Galloway (2006).

The hypothesis that the ancestral Tennessee crossed the state of Mississippi is not novel. Several authors, including Hayes and Campbell (1894), Grim (1936), Brown (1967) and Isphording (1983) have also suggested that the ancestral Tennessee crossed the state of Mississippi, though the timing and placement of the courses are somewhat different. Hayes and Campbell (1894) believed that during the Tertiary, the pirated ancestral Sequatchie River flowed across Mississippi towards the Mississippi Embayment following the course of the modern Big Black River. The ancestral Sequatchie maintained this course until it was captured and turned north forming the modern course of the Tennessee River (Fig. 2.3). Grim (1936) concurred with Hayes and Campbell (1894) citing petrographic and mineralogic similarities between the Wilcox and Midway formations to those of the southern Appalachians and believed that the Wilcox and Midway were deposited in the delta of the ancestral Tennessee (Grim 1936). Brown (1967) extended this hypothesis suggesting that the ancestral Tennessee crossed the state of Mississippi with an outlet in southwest Mississippi between the modern Homochitto and Amite Rivers.

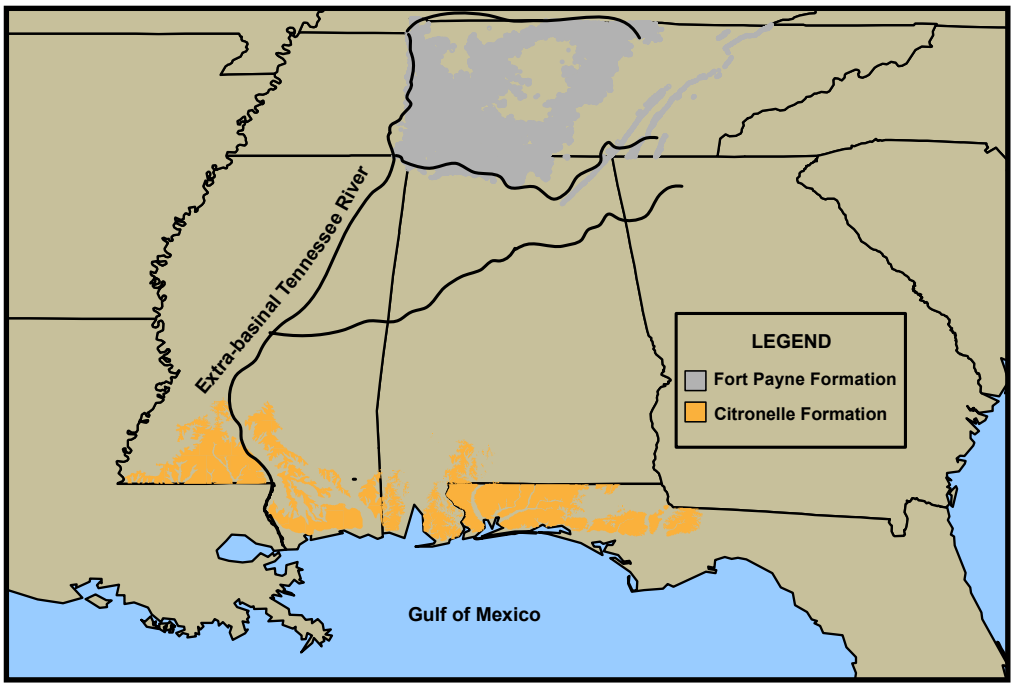


Fig. 2.2. Extra-basinal Tennessee River system. Modified from Galloway (2005) and Combellas-Bigott and Galloway (2006).

Fig. 2.3. Course of the Tertiary Tennessee River as proposed by Hayes and Campbell (1894). Modified from Chamberlin and Salisbury (1905).

In support of this hypothesis, Brown (1967) suggested that the gravels of the Citronelle Formation were part of the ancient stream bed; however, Isphording (1983) examined Miocene coastal deposits including a salt dome near New Augusta, Mississippi and determined that the dome contained a suite of metamorphic minerals that were most likely derived from the Appalachian Piedmont. These minerals were absent from adjacent formations, leading Isphording (1983) to hypothesize that once it reached Guntersville, Alabama, the Tennessee River continued in southwesterly course across Alabama and into the Pascagoula River Basin in Mississippi (Fig. 2.4).

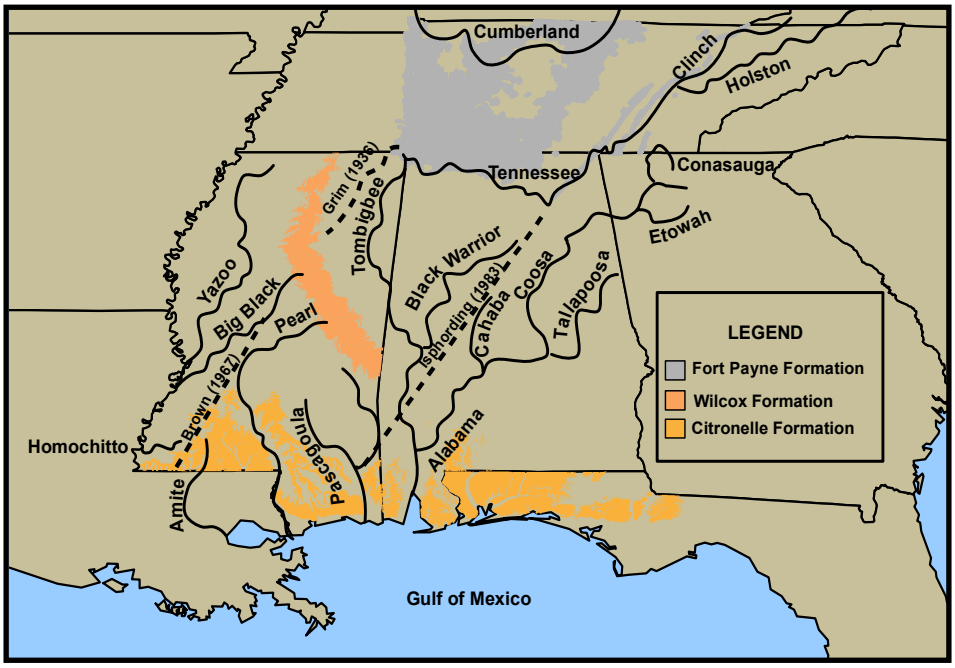


Fig. 2.4. Course of the ancestral Tennessee based on Grim (1936), Brown (1967) and Isphording (1983).

In investigations of the Citronelle Formation in the Florida Parishes of Louisiana (Self, 1983, 1986) and in Marion County, Mississippi (Smith and Meylan, 1983), it was noted that the formation was predominated by chert gravels. The chert gravels are typically weathered, subangular to subround in shape, and may contain Palaeozoic fossils (Self, 1983; Smith and

Meylan, 1983). These detrital gravels may have been deposited by the Mississippi River or the ancestral Tennessee River (Carlston, 1950; Potter 1955a, 1955b; Doering, 1956; Smith and Meylan, 1983; Guccione, 1984; Self, 1986; Russell, 1987; Self, 1993; Combellas-Bigott and Galloway, 2002; Galloway, 2005; Combellas-Bigott and Galloway, 2006). Detailed analyses of heavy minerals in the Citronelle, however, strongly support an Appalachian source for the Citronelle sediments suggesting that they were deposited by the ancestral Tennessee River (Rosen, 1969). Further, the abundance of chert in the Citronelle also suggests an Appalachian source, as the Mississippian Fort Payne Formation is the most proximal source of chert (Smith and Meylan, 1983; Self, 1986, 1993; Dockery et al., 2008). The placement and timing of the extra-basinal Tennessee River as proposed by Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005) is somewhat a synthesis of the hypotheses that place the course of the ancestral Tennessee River across Mississippi and may explain the predominance of chert in the Citronelle Formation; therefore, based on the aforementioned research, it is hypothesized that the ancestral Tennessee River system deposited the Citronelle in Mississippi and eastern Louisiana and that the detrital cherts of the Citronelle Formation in south Mississippi were derived from the Fort Payne Formation of the Highland Rim. In order to test this hypothesis, rare earth element (REE) signatures from detrital cherts collected from Citronelle deposits of the Lower Pearl River basin and adjacent drainages in southern Mississippi were compared with REE signatures from cherts taken the Fort Payne Formation along the Highland Rim.

The Citronelle Controversies

The age and depositional history of the Citronelle have been controversial since its description by Matson (1916). These problems have persisted largely due to the similarities of the Citronelle gravels to those of adjacent formations of differing ages which has led to questions regarding whether the Citronelle is a preglacial or a glacial outwash deposit and whether the name itself is valid (May, 1980).

Synonymy and Age

The Citronelle has been recognized under the terms "Orange Sand," "stratified drift" and "Lafayette" (Hilgard, 1860, 1871; McGee, 1892; Matson [and references therein], 1916). Hilgard (1860) described the Orange Sand Formation and noted that it predominated the surface of Mississippi. The Orange Sand Formation included alluvial deposits along the Mississippi River, which are now recognized as Pleistocene in age (Fisk, 1938), and gravels of the Tuscaloosa Formation, which are now recognized as Cretaceous in age (Smith and Johnson, 1887; Needham, 1934). Subsequently, McGee (1892) included the Citronelle in his description of the Lafayette Formation. The Lafayette Formation became a catch-all term inclusive of Tertiary age coastal plain deposits from Virginia to Texas, alluvial deposits of the Mississippi River delta, and deposits along the Mississippi Embayment (McGee, 1892; Fisk, 1938; Potter, 1955a, 1955b). Berry (1916), in conjunction with Matson (1916) assigned a Pliocene age to the Citronelle based on fossil beds at Lambert and Red Bluff, Alabama that contained the following extinct plants: *Taxodium distichum, Pinus* sp., *Yucca* sp., *Hicoria* [*Carya*] *pretexana*, *Betula prenigra*, *Fagus lambertensis*, *Quercus nigra*, *Quercus catesbaeifolia*, *Quercus lambertensis*, *Quercus previrginiana*, *Planera aquatica*, *Caesalpinia citronellensis*, *Prunus* sp., *Vitis* sp., *Trapa alabamensis*, *Nyssa aquaticaformis*, *Bumelia preangustifolia*, and *Fraxinus* sp. Initially, Doering (1935; 1960), based on similarities with the coastal plain deposits equated the Pliocene Willis Formation of Texas with the Citronelle but later concluded that the Citronelle was Pleistocene in age (Doering 1956, 1958). Berry (1937) later reiterated the Pliocene age originally assigned to the Citronelle noting that the flora it contained was the most extensive of Pliocene age known from the Atlantic region; however, Roy (1939) examined the fossiliferous bed near the type locality of the Citronelle used by Berry (1916) to date the Citronelle as Pliocene and argued that the fossil plants were in an underlying clay bed that was separated from the Citronelle by faulting and an unconformity, and the Citronelle must therefore be Pleistocene in age. In an analysis of terraces along the Mississippi River, Fisk (1938, 1951) described the Pleistocene age Williana,

Bentley, Montgomery, and Prairie terraces which formed in response to interglacial highstands and considered the Citronelle the basal unit of these terraces. Trowbridge (1954) agreed with Fisk (1938, 1951) noting that the Pleistocene age assigned to the Citronelle was indisputable. Doering (1956, 1958) also considered the Citronelle to be Pleistocene in age, but in contrast to Fisk (1938, 1951), considered it a preglacial basal deposit. Stringfield and LaMoreaux (1957) disputed the Pleistocene age assigned to the Citronelle, stating that Roy (1939) and Doering (1958) failed to examine the fossil bed at Red Bluff, Perdido Bay, Baldwin County, Alabama that was also used by Berry (1916) to date the Citronelle Formation. Stringfield and LaMoreaux (1957) further noted that the Citronelle in Florida was overlain by the oldest Pleistocene marine terrace, which indicated that the Citronelle must be Pliocene in age. Alt and Brooks (1965), however, based on soil associations, assigned a Miocene age to the Citronelle in Florida. Isphording and Lamb (1971) concurred with Stringfield and LaMoreaux (1957) when they described an assemblage of vertebrates from the base of the Citronelle along Chickasabogue Creek, Mobile County, Alabama. Fossils included both marine and terrestrial animals such as Scombroid fishes, turtles, a crocodile, horses, a rhinoceros, and a river dolphin. These fossils were dated as mid-Pliocene, which led Isphording and Lamb (1971) to assign a Pliocene age to the Citronelle. Based on pollen from the Japanese umbrella pine (genus *Sciadopitys*) found in Citronelle deposits in Mississippi and Florida, Otvos (1998 [and references therein]) concurred with Isphording and Lamb (1971) and assigned a Pliocene age to the Citronelle. This pine is currently endemic to Japan but was formerly distributed in North America from the Cretaceous until its extinction in the Pliocene (Otvos, 1998 [and references therein]). The age controversy still persists perhaps due to ages being assigned in studies of localized sections of the Citronelle. Despite these age issues, the timing of deposition still correlates with the timing of the extra-basinal Tennessee River of Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005), and may still provide evidence that the ancestral Tennessee River had a direct outlet to the GOM via a course across the state of Mississippi.

Stratigraphy

The Citronelle has been characterized as a blanket (i.e., continuous layer) deposit that has been dissected by modern fluvial systems (Isphording and Lamb, 1971; Meylan and Li, 1995), but May (1980) and May et al. (1995) have suggested that the Catahoula, Hattiesburg, Pascagoula and Citronelle are all facies of a single non-marine offlapping complex with multi-sourced deposits. The Citronelle is recognizable in the subsurface and unconformably caps the highest of these coastal plain deposits and has been repeatedly dissected by various streams leading to the erosion of the overbank fines leaving behind the channel bars (Brown, 1944; May, 1980; Meylan and Li, 1995). It is unclear whether the Citronelle is a deposit formed from the re-working of the underlying gravels by these streams, from cyclical weathering and erosion which removed younger sediments and allowed older underlying sediments to surface (May, 1980), or from direct deposition on the coastal plain. Isphording (1976) employed multivariate statistics to analyze the detrital mineralogies of the Citronelle and the underlying Miocene strata. Results of a cluster analysis yielded three distinct groups including a Miocene sample group, a Citronelle group, and a mixed group that contained both the Miocene and Citronelle, and the results of a discriminant analysis showed that the Citronelle and Miocene samples were statistically significantly different. Isphording (1976) concluded the Citronelle could be differentiated based on multivariate analyses of its mineralogy and that the mixed group was present because the Citronelle was derived from the reworking of the underlying Miocene sediments. Similar to Isphording (1976), Li and Meylan (1994) have argued that a combination of field mapping and laboratory data such as grain size statistics, sand grain petrography, and clay mineralogy can be used to identify and map the Citronelle as a separate, distinct stratigraphic unit. Further, Dockery (1995) disagreed with what he termed the "wastebasket" nature of the Citronelle as proposed by May et al. (1995) and argued that the Citronelle cannot be part of a large complex because most of the Citronelle outcrops are to the south of the Catahoula exposures and therefore cannot be an updip facies of that unit, and also, most of the Citronelle is underlain by the Hattiesburg, a formation that contains few gravels.

Local sections of the Citronelle have been characterized in detail and the results of these analyses have been used to generalize the stratigraphical framework for the entire formation, but it is rarely noted that the character of the local sections that have been described may be a result of local influences that did not necessarily affect the other sections which makes direct correlations between the localized sections difficult.

Depositional Environment and General Characteristics

Localized studies of the Citronelle tend to concur with the original description of the formation given by Matson (1916) which characterized the Citronelle as a fluvial deposit. For example, Doering (1935) described the Willis Formation in Texas, which was later equated to the Citronelle (Doering, 1960), and suggested that the sediments of the Willis were deposited by streams that had cut into the underlying Catahoula Formation. The Willis Formation was generally characterized as a coarse, red sand bearing quartz and chert gravels (Doering, 1935).

Self (1983, 1986) examined the Citronelle Formation in southeastern Louisiana and noted that the deposits contain red, sandy gravel beds with a high chert content. The Citronelle gravels are coarser and more poorly sorted than the overlying alluvial gravels. Further, the gravel beds of the Citronelle were characterized as either massively bedded with interstitial sand with some foreset beds, as channel fill gravels, or as interbedded sand and gravels representing the longitudinal bars of a braided stream system, which suggested that the Citronelle of southeastern Louisiana was deposited by braided streams along an alluvial fan (Self 1983, 1986).

In an investigation of the Citronelle Formation at Red Bluff, Marion County, Mississippi, Smith and Meylan (1983) determined that the outcrop was approximately one-half sand and one-half gravel. The gravels were predominantly poorly sorted cherts found in facies containing cross-bedded palaeochannels. Based on this evidence, Smith and Meylan (1983) concluded that this section of the Citronelle was also deposited by a braided stream system.

Otvos (2004) examined the Citronelle from southeastern Louisiana to Florida and included sites near the Gulf Coast waters. The deposits included fluvial sands and gravels, floodplain

deposits, and estuarine influenced deposits. Muddy deposits were found in areas interpreted as floodplains which led Otvos (2004) to suggest that anastomosed and meandering stream deposition should also be considered for some sections of the Citronelle. Further, Otvos (2004) advocated further highly detailed studies of the Citronelle that include the recognition that differing fluvial depositional styles may be present and the mapping of individual stream basins with attention to paleochannel configurations. Such studies could provide insight regarding the ancestral river systems that crossed the coastal plain not only the state of Mississippi, but also its neighbors.

Provenance

Both the Mississippi and Tennessee Rivers have been proposed transporters of the sands and gravels of the Citronelle. Hilgard (1871) favored a Mississippi River transport stating that the pebbles were derived from a northern source and carried by "a southward flow of waters, of considerable violence" (p. 517). Carlston (1950) suggested that the chert gravels in the Citronelle of western Alabama and Mississippi were deposited by the Mississippi River as they could not have been deposited by any of the modern rivers based on their courses. Potter (1955a, 1955b) suggested that the gravels of the Citronelle were derived from the Lafayette Formation in the upper Mississippi River valley. Guccione (1984), however, suggested that the Citronelle gravels were derived from the gravels of Crowley's Ridge in Arkansas. Russell (1987) has argued that the ancestral Tennessee River was a tributary to the ancestral Mississippi River system and was responsible for deposition of both the gravels along the Mississippi River and the Citronelle. Based on a comprehensive dataset that included heavy mineral and fossil analyses, Smith and Meylan (1983) suggested that the sediments of the Citronelle of Red Bluff, Marion County, Mississippi were derived from the deposits of the Highland Rim and Black Warrior Basin in Alabama. Fossils recognized by Smith and Meylan (1983) include crinoids, brachiopods, bivalves (pelecypods), bryozoans, and corals and similar fossils have been recognized in other sections of the Citronelle (Dockery, 1996). Further, the findings of Smith and Meylan (1983) are

similar to the results of mineralogical analyses of the Citronelle reported by Rosen (1969) and Pirkle et al. (1985) and for older coastal plain deposits (Needham, 1934; Grim, 1936; Todd and Folk, 1957; Isphording, 1983) which strongly support the hypothesis that the Citronelle sediments were derived from an Appalachian source. Further, these findings suggest that the cherts found in the Citronelle were also derived from an Appalachian source, and the most proximal source of chert is found in the Fort Payne Formation.

The Fort Payne Formation

With deposits ranging from the Illinois Basin into western Kentucky through central Tennessee into northern Alabama and Georgia, the Fort Payne Formation (Mississippian) marks the transition from the anoxic conditions represented by the Chattanooga shale to the shallow carbonate shelf of the St. Louis limestone (Lumsden, 1988). Deposition of the Fort Payne occurred along the Palaeozoic continental margin near the Ouachita salient on marine ramps in quiet waters that were 10-100 meters deep (Thomas, 1976; Lumsden, 1988; Meyer et al., 1995). The Fort Payne is mainly composed of chert that formed from the devitrification of opal derived from sponges and occurs as both nodules and beds in limestone facies and as stand-alone massive beds composed of interlocked silica and calcite (Marcher, 1962; Lumsden, 1988). Dolomite, calcite, and quartz sands are also present in some portions of the formation (Lumsden, 1988). Though not prevalent, fossils recognized in the Fort Payne include crinoid stems, bryozoan fragments, brachiopods, ostracods, and sponges (Marcher, 1962; Lumsden, 1988). Similar fossils have been reported from the Citronelle Formation (Smith and Meylan, 1983) and suggest that the chert in the Citronelle may have been derived from the Fort Payne chert. Rare earth element (REE) signatures from the Fort Payne could help to determine the validity of this hypothesis, and would further help to support or refute the placement and timing of the ancestral Tennessee River proposed by Galloway (2005) and Combellas-Bigott and Galloway (2002, 2006).

Use of REE Signatures to Determine Chert Provenance

Rare earth elements (REEs) can be used determine the depositional environment and provenance of sedimentary rocks such as chert due to their low solubility and low mobility which allow them to be incorporated into detrital sediments without major alteration of their concentrations, thus preserving a record of their protolith concentrations in the sediments (Taylor and McLennan, 1981; Murray et al., 1991, 1992; Murray, 1994; Owen et al., 1999). Chert, in particular, is highly resistant to weathering and diagenetic effects, and their REE concentrations typically remain stable in their post-depositional environments (Shimizu and Masuda, 1977; Murray et al., 1990; Murray et al., 1991; Murray, 1994; Owen et al., 1999).

REE concentrations are typically normalized against a standard of REE concentrations found in a chemically immobile source rock representative such as chondrites (Shimizu and Masuda, 1977; Anders and Grevesse, 1988; Morey and Setterholm, 1997; Owen et al., 1999) or the North American Shale Composite (NASC) (Gromet et al., 1984; Murray, 1994). Normalization removes the inherent odd-even variability in the atomic numbers that arises from variations in the binding energy of the nucleus (Elderfield, 1988) allowing for direct comparison of the REE concentrations in detrital samples to its supposed unaltered protolith (Murray et al., 1992; Morey and Setterholm, 1997; Owen et al., 1999). The normalized concentrations are calculated by dividing each REE concentration in each sample under investigation by the corresponding REE concentration in the selected standard (e.g. La_{sample}/La_{shale}……Lu_{sample}/Lu_{shale}) (Gromet et al., 1984; Murray et al., 1990; Owen et al., 1999). A normalized REE pattern is typically flattened because the REEs tend to behave as a cohesive group due to a reciprocal relationship whereby an increase in the atomic number corresponds to an increase in the filling of 4f shell and a concomitant decrease in the atomic and ionic radii leading to the occlusion of the 4f electrons from the conduction band found in other metals effectively limiting the differences in chemical reactivities among the REEs (Cox et al., 1981; Elderfield, 1988; Jia, 1991). The cohesive behavior occurs when the REEs are in their stable trivalent state, but cerium (Ce) and europium

(Eu) may show either negative or positive peaks because they can be selectively enriched or depleted depending on the environment (Taylor and McLennan, 1988; Murray et al. 1992). These behaviors are respectively known as the Ce anomaly (Ce/Ce*) and the Eu anomaly (Eu/Eu*) where Ce* and Eu* represent the theoretical value of having no anomaly, and these anomalies can be used to determine the depositional environment and provenance of non-metamorphosed rocks such as chert (Shimizu and Masuda, 1977; Taylor and McLennan, 1988; Murray et al., 1990; Bau, 1991; Murray et al., 1991; Murray et al., 1992; Owen et al., 1999)

Most of the REEs are trivalent (Table 2.1), but in some aqueous environments with oxidizing conditions, Ce will oxidize to its insoluble tetravalent solid phase (Elderfield, 1988). This Ce anomaly (Ce/Ce*) reflects the normalized Ce abundances relative to normalized lanthanum (La) and either praseodymium (Pr) or neodymium (Nd) concentrations (Elderfield, 1988; Murray et al., 1990; Murray et al., 1991; Murray, 1994). Owen et al. (1999) have shown that the Ce anomaly can be calculated as follows:

$$\text{Ce anomaly} = Ce_n/Ce^* \text{ where } Ce^* = (La_n + Pr_n)/2$$

$$n = \text{normalized concentration}$$

Similarly, Eu has a trivalent form, but under certain temperature, pH, and redox conditions, especially in the oceans, it can exist in its divalent form and substitute for calcium (Ca) in silicate minerals such as plagioclase (Weill and Drake, 1973; Elderfield, 1988; Bau, 1991). As with the Ce anomaly, the Eu anomaly (Eu/Eu*) reflects the normalized Eu values relative to its neighbors samarium (Sm) and gadolinium (Gd). Owen et al. (1999) have shown that the Eu anomaly can be calculated as follows:

$$\text{Eu anomaly} = Eu_n/Eu^* \text{ where } Eu^* = (Sm_n + Gd_n)/2$$

$$n = \text{normalized concentration}$$

Taylor and McLennan (1988), however, argue that taking the arithmetic means of the lanthanides neighboring Ce and Eu is incorrect and results in misleading patterns especially in chondrite normalized data that exhibit a steep pattern. To prevent this problem, Taylor and McLennan (1988) argue that the geometric means the neighbors of Ce and Eu should be used instead. The geometric means may be calculated as follows:

$$\text{Ce anomaly} = Ce_n/Ce^* \text{ where } Ce^* = \sqrt{(La_n \cdot Pr_n)}$$

n = normalized concentration

$$\text{Eu anomaly} = Eu_n/Eu^* \text{ where } Eu^* = \sqrt{(Sm_n \cdot Gd_n)}$$

n = normalized concentration

Anomaly values that are < 1 are considered negative and reflect a depletion of Ce and Eu relative to the other REEs; whereas, a value > 1 indicates an enrichment of Ce and Eu relative to the other REEs. Shimizu and Masuda (1977) suggest that a small positive or the lack of a Ce anomaly are indicative of cherts exposed on land, while the behavior of Ce in shallow seas conformed to that of the other REEs, and Ce was selectively depleted relative to the other REEs in deep-sea environments. Further, Shimizu and Masuda (1977) and Elderfield (1988) suggest that a negative Eu anomaly is indicative of continentally derived materials that are delivered to the ocean basins via fluvial and aeolian deposition. Conversely, a positive Eu anomaly is associated with waters that have been in contact with mid-oceanic ridge basalts (MORB) and with acidic fluid-rock interactions where the REE pattern of the liquid is dependent upon sorption mechanisms and Eu occurs in its divalent state (Bau, 1991).

Murray et al. (1991) have further summarized Ce/Ce* values for non-carbonitic sediments and suggest that Ce/Ce* values that cluster around ~ 1 reflect terrigenous sedimentary input, low

Ce/Ce* values between ~ 0.1 and 0.4 are indicative of ridge-proximal deposition, while Ce/Ce* values for pelagic sediments can range between ~ 0.2 and 1.2.

Table 2.1

Selected Characteristics of the REEs

Name	**Symbol**	**Atomic Number**	**Atomic Weight**	**Valence**
Lanthanum	La	57	138.91	3
Cerium	Ce	58	140.12	3, 4
Praseodymium	Pr	59	140.907	3
Neodymium	Nd	60	144.24	3
Promethium	Pm	61	147	3
Samarium	Sm	62	150.35	2, 3
Europium	Eu	63	151.96	2, 3
Gadolinium	Gd	64	157.25	3
Terbium	Tb	65	158.924	3
Dysprosium	Dy	66	162.50	3
Holmium	Ho	67	164.930	3
Erbium	Er	68	167.26	3
Thulium	Tm	69	168.934	3
Ytterbium	Yb	70	173.04	2, 3
Lutetium	Lu	71	174.97	3

In addition to depositional environment, Murray et al. (1992) and Owen et al. (1999) have shown that comparison of the Ce anomaly to the Eu anomaly can be used to determine the provenance of chert samples, and further resolution of provenance can be obtained by plotting the Eu anomaly values against the ratio of light REEs (LREEs (La-Sm)) to heavy REEs (HREEs (Gd-Lu)). The ratio of light to heavy REEs is calculated by dividing the normalized La concentrations by the normalized ytterbium (Yb) concentrations (La_n/Yb_n) (Murray et al., 1992; Owen et al., 1999).

McLennan et al. (1993) have shown that the relative enrichment or depletion of the HREEs can be determined by the normalized gadolinium/ytterbium (Gd_n/Yb_n) ratio. Higher ratios are indicative of a relative depletion in the HREEs.

Materials and Methods

To test the hypothesis that detrital chert(s) within the Citronelle Formation of Mississippi are remnants of the Fort Payne Formation which were deposited by the ancestral Tennessee River, chert samples were taken from Citronelle outcrops in south Mississippi, from Fort Payne outcrops in Alabama and Tennessee, and from the Gordo Gravel member of the Tuscaloosa Formation in Alabama. Additional chert samples were taken from a streambed near each of the formations, but the proximity of the stream to the formation does not necessarily subscribe that the samples were derived from the formation as they could be transported from a differing formation upstream.

Sampling Localities

Detrital (allochthonous) cherts from the Citronelle Formation were sampled from four localities in Mississippi. One sample was taken from the streambed of Bayou Pierre (BP), which currently flows into the Mississippi River. Two samples, Topisaw Creek (TC) and Mad Dog Hill (MDH) were taken from exposed outcrops in the Pearl River basin, and the final sample was taken from a gravel quarry at Camp Shelby (CS), which is in the Pascagoula River basin (Fig. 2.5; Table 2.2). The Camp Shelby gravels contained coral fossils (identified by the author), but fossils were not present in the other samples.

Two in-situ chert (autochthonous) samples and one detrital (allochthonous) chert sample were also taken from the Fort Payne Formation. One sample was taken in Alabama, and the remaining two samples were taken from the upper Tennessee River Basin along the western Highland Rim.

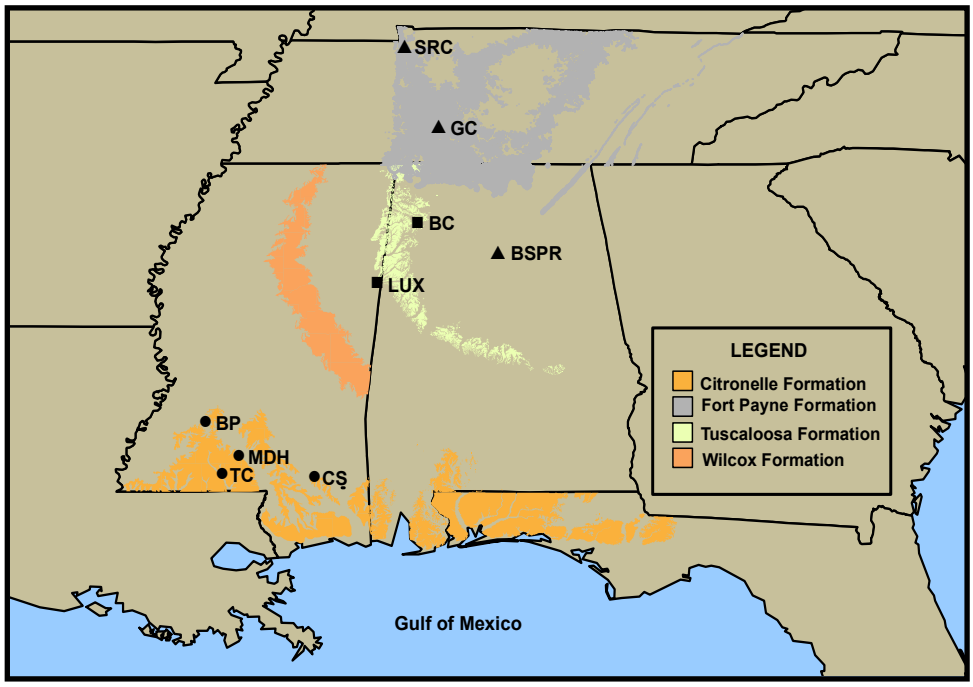


Fig. 2.5. Map of chert collecting localities.

Table 2.2

Identification and Collecting Localities of the Chert Samples

Identification	Collecting Locality	Formation
BP	Bayou Pierre streambed, Copiah County, MS	Citronelle Formation
CS	Camp Shelby gravel quarry, Perry County, MS	Citronelle Formation
MDH	Mad Dog Hill outcrop, Lawrence County, MS	Citronelle Formation
TC	Topisaw Creek outcrop, Pike County, MS	Citronelle Formation
BSPR	Blount Springs outcrop, Blount County, AL	Fort Payne Formation
GC	Grinders Creek streambed, Lewis County, TN	Fort Payne Formation
SRC	Standing Rock Creek outcrop, Stewart County, TN	Fort Payne Formation
BC	Bear Creek bridge on HWY 17, Franklin County, AL	Tuscaloosa Formation
LUX	Luxapalila Creek streambed, Lowndes County, MS	Tuscaloosa Formation

The first in-situ sample was collected near Blount Springs, Alabama (BSPR). This sample represents a chert nodule formed in a limestone rather than a bedded chert as found along the northern Highland Rim. The detrital sample was taken from the streambed of Grinders Creek (GC) in Tennessee, and the last in-situ sample was taken from an exposed outcrop of bedded chert along Standing Rock Creek (SRC) in Tennessee (Fig. 2.5; Table 2.2; Appendix A).

In addition to the samples taken from the Citronelle and Fort Payne Formations, two detrital (allochthonous) chert samples were taken from the Tuscaloosa Formation due to its similarity to the Citronelle. The first sample was taken from the streambed of Luxapalila Creek (LUX) in Mississippi, which is in the Tombigbee River basin, and the second sample was collected from an outcrop exposed along Highway 17, south of the bridge across Bear Creek (BC) in Alabama, which is in the lower Tennessee River basin (Fig. 2.5; Table 2.2).

Data Processing and Analysis

Three samples from each locality were sent to the University of Southern Mississippi Center for Trace Analysis, Department of Marine Science, Stennis Space Center, Mississippi where they were prepared for and analyzed using inductively coupled plasma – mass spectrometry (ICP-MS) to determine the abundances of each REE in each sample. The returned concentrations were normalized against both the NASC (Gromet et al. 1984) and the chondrite data of Anders and Grevesse (1989). Following normalization, the Ce anomaly, Eu anomaly were calculated using the arithmetic mean (Owen et al. 1999) and the geometric mean (Taylor and McLennan, 1988). In addition, the LREE/HREE ratio and HREE depletion were also calculated from the sample means. An analysis of similarity (ANOSIM) plotting the LREE/HREE ratio on axis 1 against the Eu anomaly values on axis 2 was performed using the R statistics package (www.r-project.org) to determine the similarity/dissimilarity of both the formations and the individual samples.

Results

The raw REE concentrations and detection limits are given in Table 2.3, and both the arithmetic and geometrically derived shale and chondrite normalized Ce anomalies, Eu anomalies

and LREE/HREE ratios data are provided in Tables 2.4 and 2.5 respectively. REE patterns for both the shale and chondrite normalized concentrations are similar (Fig. 2.6). Both patterns show a negative Ce anomaly, which is indicative of the oxidation of soluble trivalent Ce to insoluble tetravalent Ce (Murray et al., 1991), and a slight negative Eu anomaly, which is indicative of continental input into the marine sediments (Shimizu and Masuda, 1977; Elderfield, 1988). The Eu anomaly is more pronounced on the chondrite normalized plot. With the exception of the sample taken from the streambed of Luxapalila Creek, all of the shale normalized samples show a decrease in concentration from the LREEs to the HREEs; however, the chondrite normalized data shows a decrease in the concentrations of all samples from the LREEs to the HREES, with the HREEs from each sample exhibiting the expected flat smooth pattern obtained from normalized data.

Both the arithmetically and geometrically shale and chondrite normalized scatter plots of the Ce anomaly against the Eu anomaly have a similar pattern (Figs. 2.7 and 2.8). On each of the plots, the samples tend to cluster based on the formation they were taken from. The Citronelle Camp Shelby sample, however, clusters with the samples taken form the Fort Payne Formation suggesting that the Camp Shelby sample represents chert that was re-worked from the Fort Payne.

The plots of the LREE/HREE ratios against the Eu anomaly are similar to the Ce anomaly/Eu anomaly plots whether derived using the arithmetic means or the geometric means (Figs. 2.9 and 2.10). Both the shale and chondrite normalized plots show a Fort Payne cluster that includes the Citronelle sample taken from Camp Shelby. The Citronelle samples taken from Bayou Pierre and Topisaw Creek also cluster together; however, the samples taken form the Tuscaloosa Formation do not cluster together. The sample taken from the streambed of Luxapalila Creek has an Eu anomaly that is intermediate to the Fort Payne and Citronelle clusters, while the sample taken from Bear Creek has an Eu anomaly and LREE/HREE ratio similar to the Citronelle sample taken from Mad Dog Hill. HREE depletion is most pronounced in the Bear Creek and Mad Dog Hill samples (Fig. 2.11).

Results of the ANOSIM show that the three formations can be delineated by their REE signatures. With the exception of the Camp Shelby sample, the Fort Payne is significantly different from both the Citronelle and the Tuscaloosa; however, considerable overlap exists between the REE concentrations in the Citronelle and the Tuscaloosa possibly due to the proximity of the Luxapalila Creek samples to the Topisaw Creek and Bayou Pierre samples on the plot comparing the Ce* and Eu* anomalies, and the increased HREE depletion noted in the Mad Dog Hill and Bear Creek samples.

Table 2.3

Raw Rare Earth Element Concentrations in ppm (µg/g)

Sample	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu
BC-1	9.96	9.46	1.402	4.050	0.565	0.112	0.492	0.071	0.441	0.087	0.257	0.039	0.260	0.038
BC-2	3.12	6.50	0.500	1.517	0.222	0.042	0.162	0.020	0.105	0.017	0.045	0.006	0.044	0.006
BC-3	26.51	39.26	5.295	16.644	2.239	0.410	1.651	0.214	1.183	0.191	0.423	0.047	0.263	0.032
BP-1	1.95	2.10	0.474	1.687	0.326	0.066	0.258	0.038	0.225	0.040	0.111	0.016	0.105	0.014
BP-2	2.93	2.79	0.497	1.641	0.316	0.057	0.220	0.043	0.230	0.040	0.104	0.015	0.094	0.013
BP-3	1.38	0.87	0.231	0.718	0.113	0.024	0.096	0.013	0.079	0.015	0.042	0.006	0.036	0.005
BSPR-1	0.34	0.44	0.081	0.359	0.072	0.015	0.075	0.010	0.061	0.013	0.036	0.005	0.032	0.005
BSPR-2	0.56	0.60	0.137	0.604	0.124	0.027	0.133	0.017	0.105	0.022	0.059	0.007	0.045	0.007
BSPR-3	0.38	0.49	0.091	0.399	0.080	0.017	0.085	0.011	0.070	0.015	0.042	0.006	0.036	0.005
CS-1	0.91	1.62	0.188	0.596	0.121	0.016	0.049	0.017	0.101	0.018	0.050	0.007	0.047	0.006
CS-2	0.98	1.07	0.183	0.618	0.140	0.026	0.101	0.023	0.142	0.026	0.073	0.011	0.073	0.010
CS-3	0.33	0.53	0.087	0.337	0.092	0.019	0.093	0.018	0.114	0.022	0.063	0.009	0.051	0.007
GC-1	0.28	0.26	0.054	0.219	0.045	0.011	0.063	0.010	0.065	0.014	0.040	0.005	0.031	0.004
GC-2	1.15	0.92	0.254	0.987	0.208	0.048	0.256	0.042	0.289	0.063	0.185	0.026	0.161	0.023
GC-3	0.57	0.65	0.136	0.527	0.107	0.023	0.123	0.020	0.146	0.034	0.105	0.015	0.098	0.014
LUX-1	1.77	3.18	0.489	1.964	0.507	0.123	0.572	0.103	0.686	0.141	0.421	0.066	0.445	0.063
LUX-2	7.73	12.53	1.735	6.244	1.227	0.269	1.230	0.204	1.367	0.288	0.864	0.129	0.850	0.127
LUX-3	13.51	20.48	2.331	7.495	1.639	0.396	2.105	0.395	2.940	0.694	2.212	0.331	2.184	0.330
MDH-1	0.84	0.93	0.137	0.419	0.071	0.015	0.052	0.007	0.036	0.006	0.018	0.003	0.017	0.002
MDH-2	1.05	1.36	0.183	0.560	0.091	0.018	0.071	0.010	0.058	0.011	0.032	0.005	0.034	0.005
MDH-3	47.46	44.62	8.073	24.674	3.968	0.730	2.796	0.326	1.546	0.232	0.570	0.078	0.515	0.072
SRC-1	2.25	2.80	0.462	1.858	0.342	0.070	0.358	0.048	0.303	0.066	0.195	0.027	0.168	0.025
SRC-2	3.44	4.53	0.716	2.832	0.510	0.101	0.519	0.071	0.448	0.099	0.297	0.042	0.260	0.039
SRC-3	5.24	5.37	0.989	3.956	0.724	0.151	0.779	0.107	0.664	0.149	0.430	0.059	0.359	0.054
TC-1	1.11	1.28	0.256	0.951	0.202	0.040	0.187	0.028	0.173	0.034	0.097	0.014	0.094	0.014
TC-2	27.76	29.15	4.408	13.016	2.255	0.430	1.648	0.244	1.424	0.262	0.720	0.104	0.681	0.094
TC-3	3.49	9.22	0.963	3.822	0.848	0.183	0.782	0.126	0.783	0.153	0.439	0.064	0.407	0.057
Detection Limit	0.01	0.01	0.001	0.002	0.001	0.003	0.003	0.000	0.001	0.000	0.001	0.000	0.001	0.000

Table 2.4

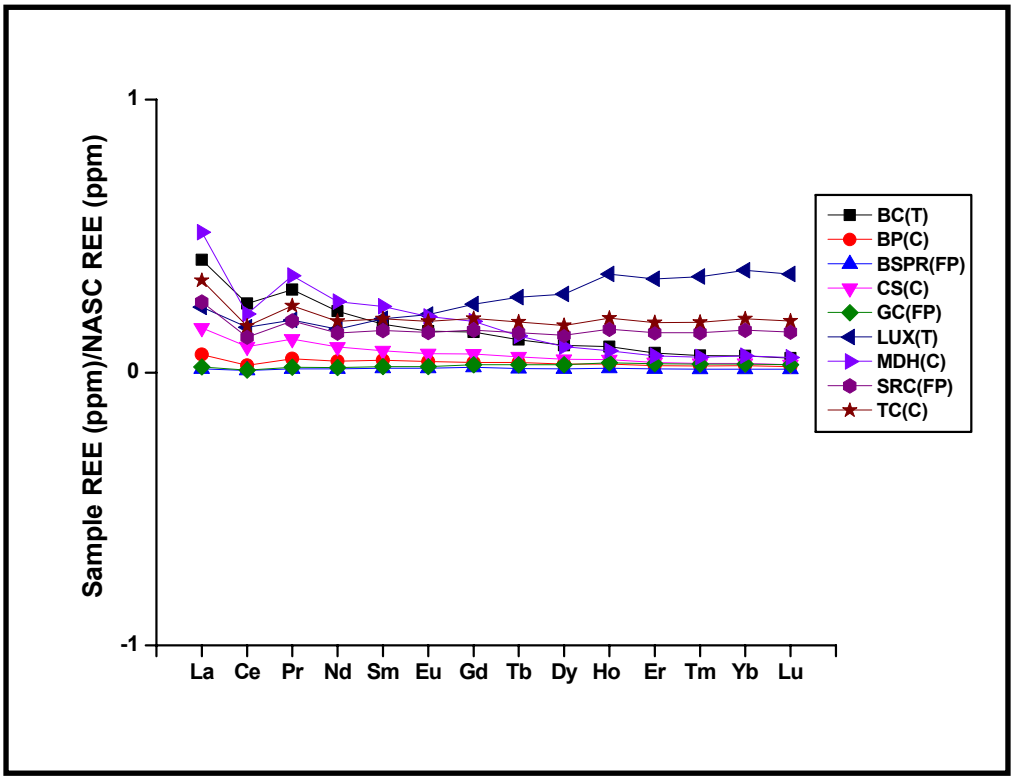
Mean NASC Normalized Arithmetically (A) and Geometrically (G) Derived Cerium and Europium Anomalies and HREE/LREE Ratios

Sample	**Ce_{sn}/Ce_{sn}*(A)**	**Eu_{sn}/Eu_{sn}*(A)**	**Ce_{sn}/Ce_{sn}*(G)**	**Eu_{sn}/Eu_{sn}*(G)**	**La_{sn}/Yb_{sn}**	**Gd_{sn}/Yb_{s}**
BC	0.704	0.935	0.712	0.939	6.764	2.423
BP	0.453	0.976	0.457	0.976	2.588	1.462
BSPR	0.532	0.891	0.532	0.894	1.087	1.537
CS	0.693	0.905	0.696	0.914	1.248	0.840
GC	0.423	0.886	0.424	0.896	0.670	0.910
LUX	0.765	0.946	0.770	0.953	0.641	0.669
MDH	0.493	0.957	0.502	0.965	8.446	3.074
SRC	0.565	0.874	0.569	0.786	1.346	1.255
TC	0.630	0.972	0.640	0.974	2.652	1.320

Table 2.5

Mean Chondrite Normalized Arithmetically (A) and Geometrically (G) Derived Cerium and Europium Anomalies and HREE/LREE Ratios

Sample	**Ce_{cn}/Ce_{cn}*(A)**	**Eu_{cn}/Eu_{cn}*(A)**	**Ce_{sn}/Ce_{sn}*(G)**	**Eu_{sn}/Eu_{sn}*(G)**	**La_{cn}/Yb_{cn}**	**Gd_{sn}/Yb_{sn}**
BC	0.7339	0.6244	0.784	0.649	48.34	3.360
BP	0.4748	0.6520	0.503	0.678	18.50	2.027
BSPR	0.5717	0.6143	0.587	0.618	7.767	2.131
CS	0.7315	0.5985	0.766	0.632	8.921	1.165
GC	0.4499	0.6193	0.466	0.620	4.788	1.262
LUX	0.8042	0.6575	0.847	0.659	4.580	0.928
MDH	0.5108	0.6349	0.553	0.667	60.36	4.261
SRC	0.5941	0.6018	0.626	0.606	9.622	1.739
TC	0.6540	0.6514	0.705	0.674	18.95	1.830



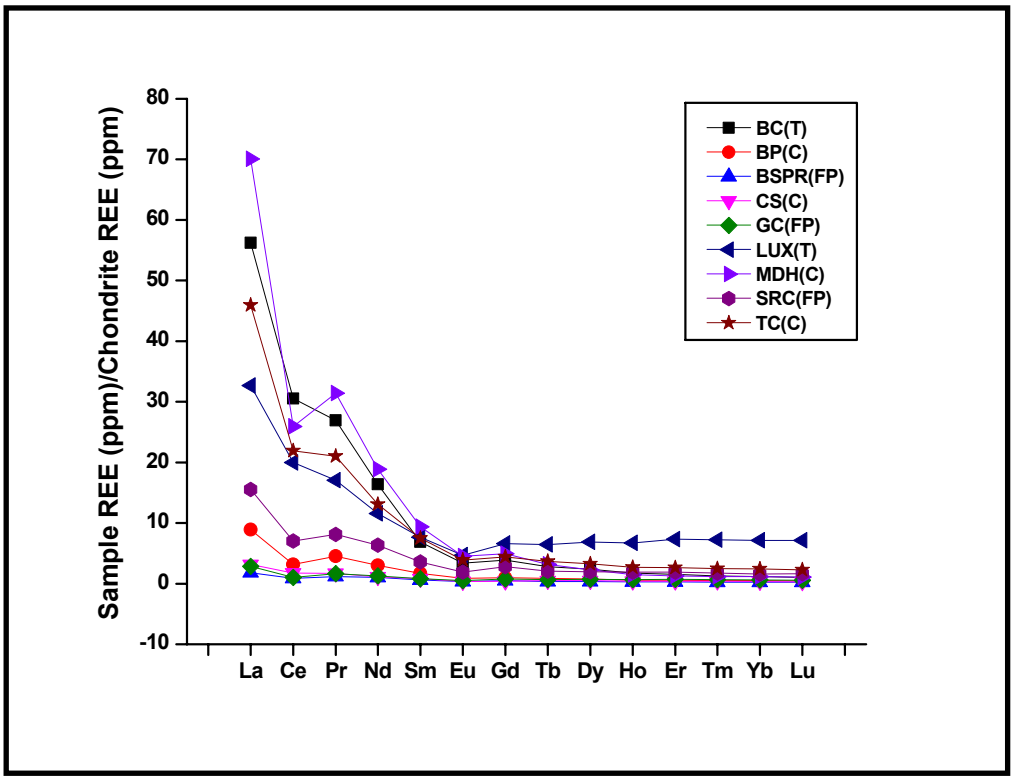
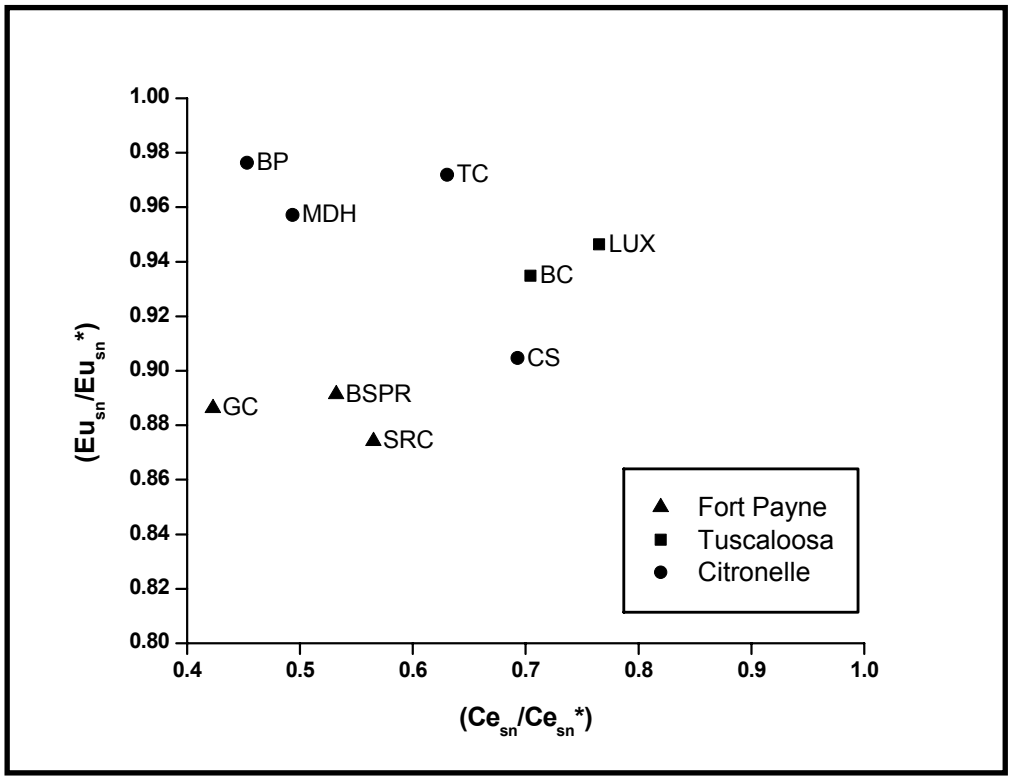


Fig. 2.6. REE concentrations for each normalized sample mean. The top graph represents the shale normalized data, and the bottom graph represents the chondrite normalized data. This outline is repeated in the following figures. Note the difference in scale between the two graphs. Legend: (FP) = Fort Payne, (T) = Tuscaloosa, and (C) = Citronelle.



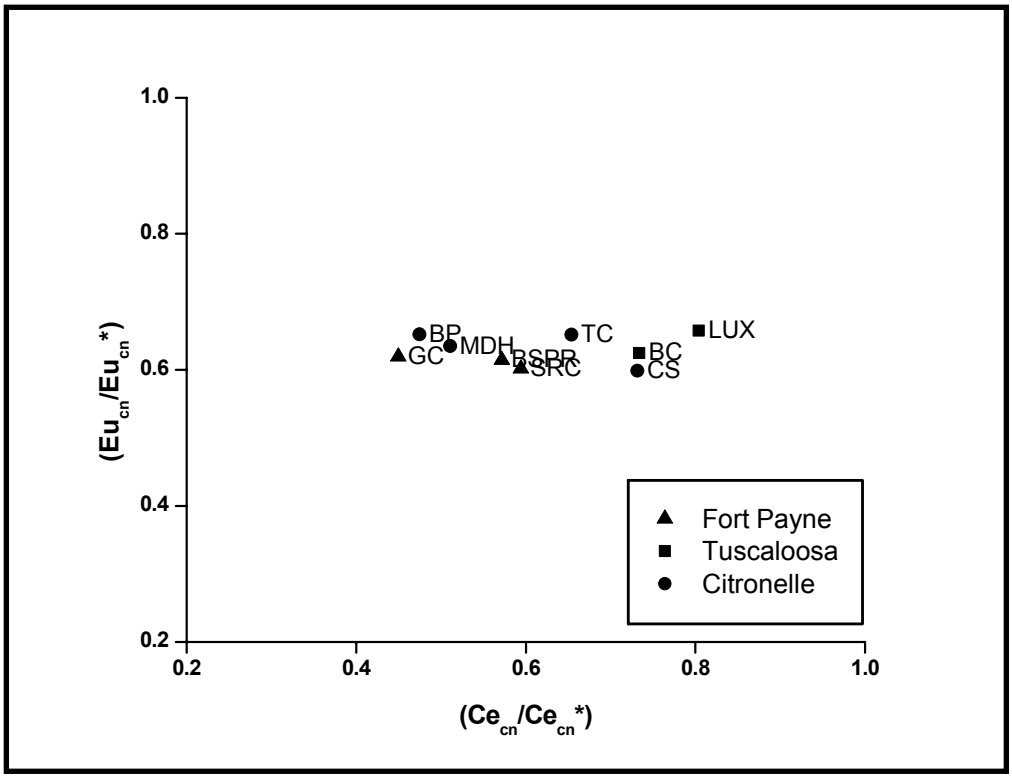


Fig. 2.7. Plots comparing the arithmetically derived Ce and Eu anomalies. Note the difference in scale between the two plots.

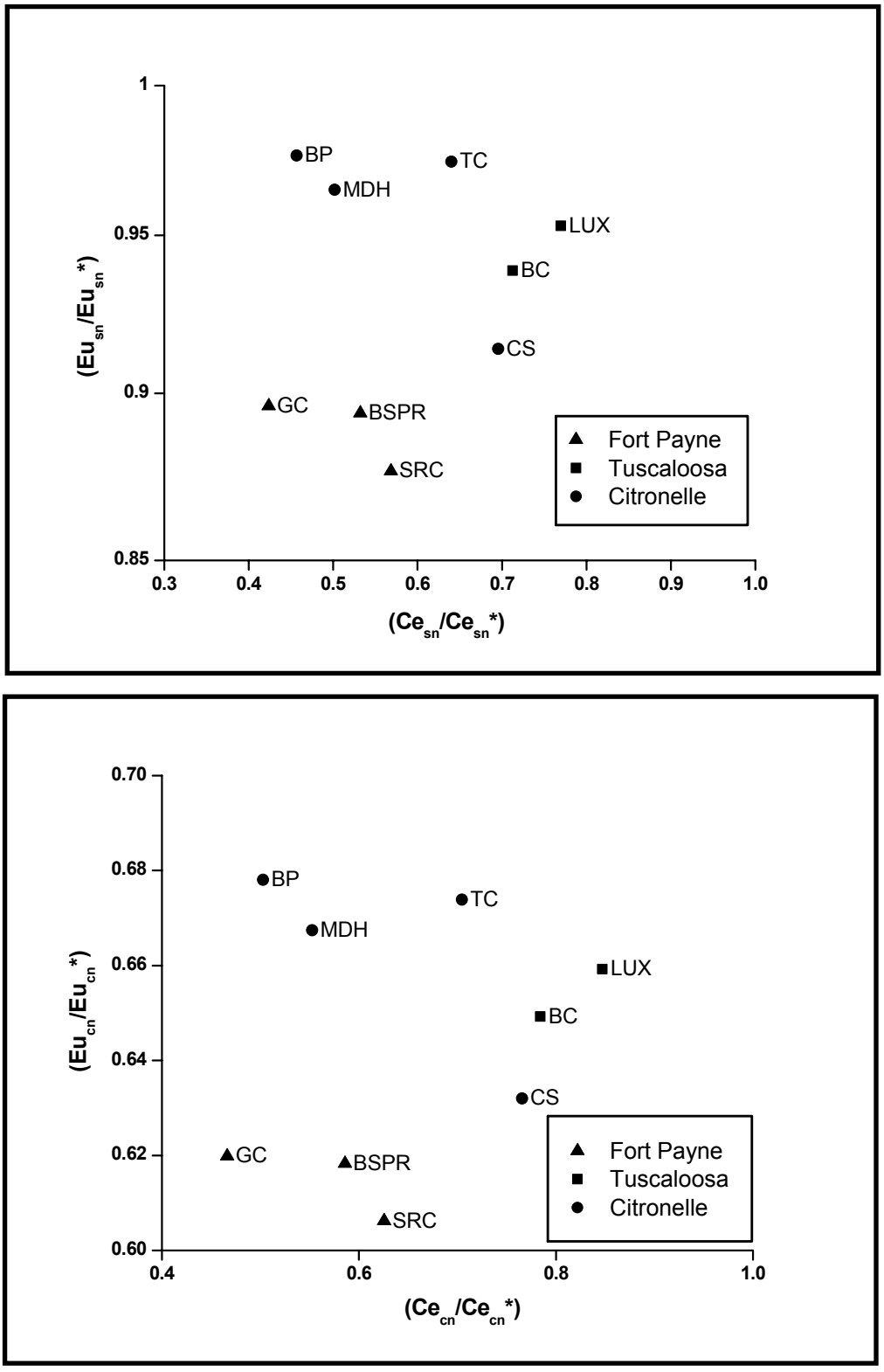


Fig. 2.8. Plots comparing the geometrically derived Ce and Eu anomalies. Note the difference in scale between the two plots.

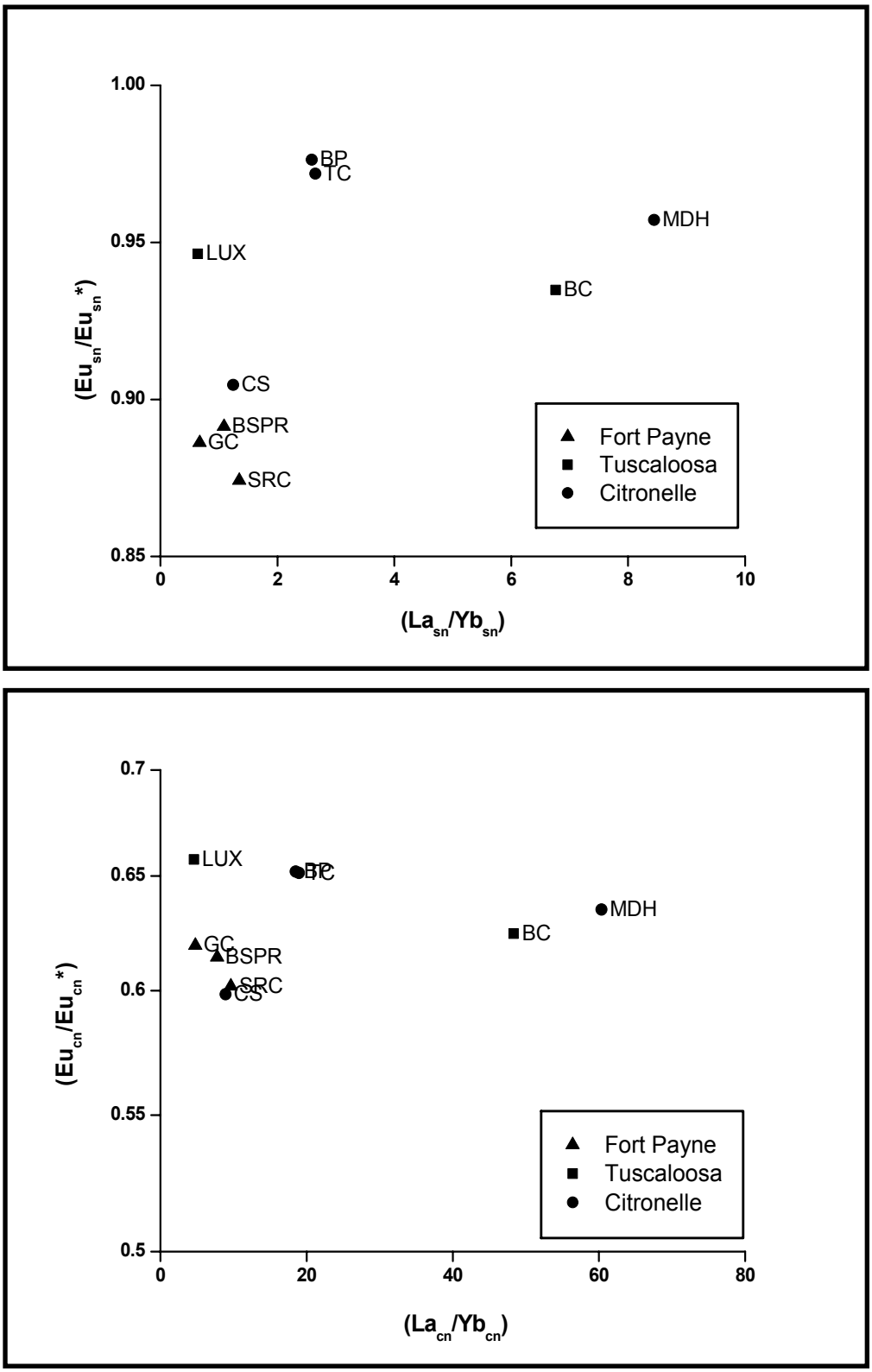
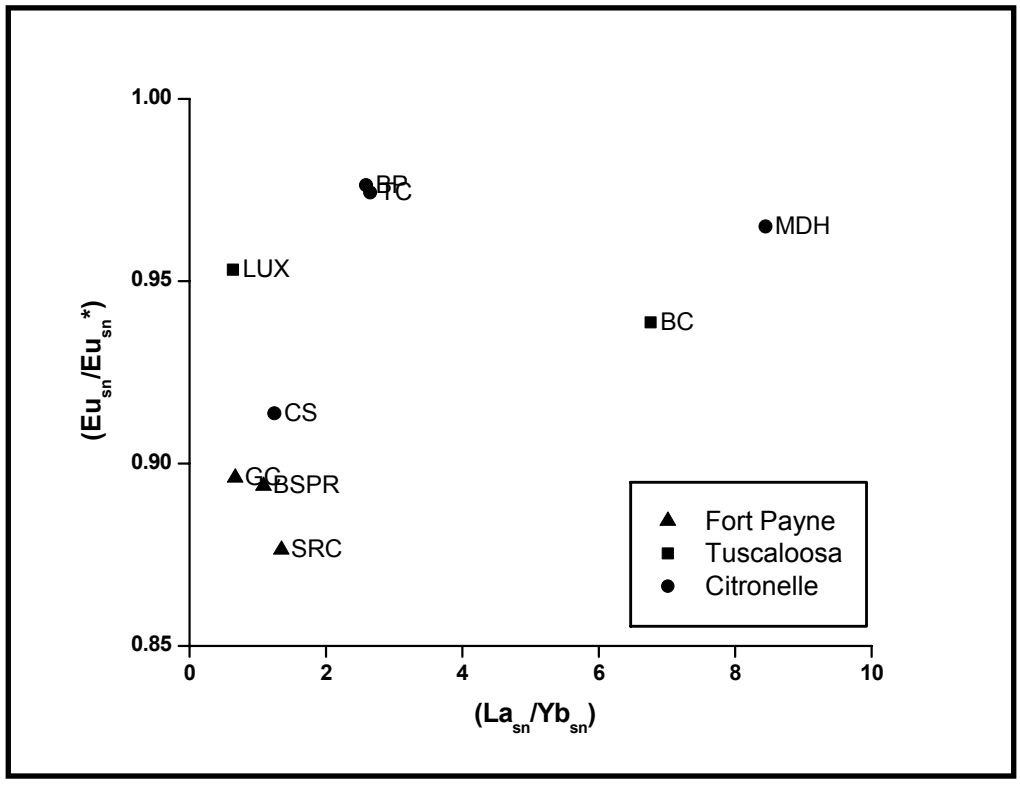


Fig. 2.9. Plots comparing the LREE/HREE ratio to the arithmetically derived Eu anomaly. Note the difference in scale between the two plots.



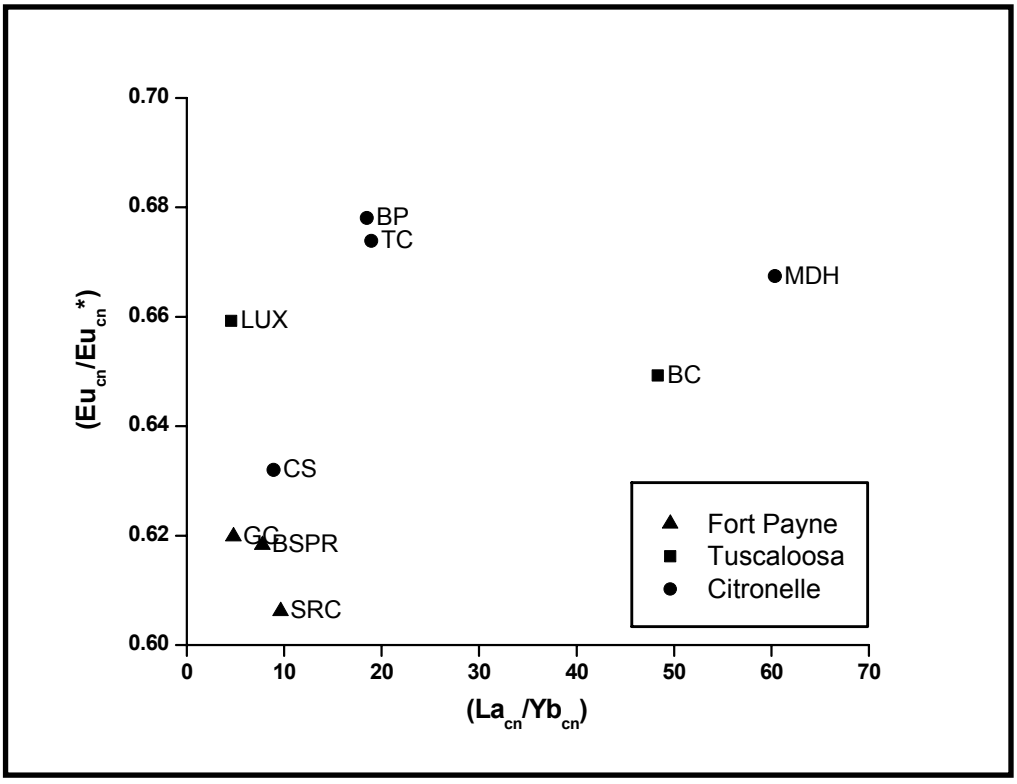


Fig. 2.10. Plots comparing the LREE/HREE ratio to the geometrically derived Eu anomaly. Note the difference in scale between the two plots.

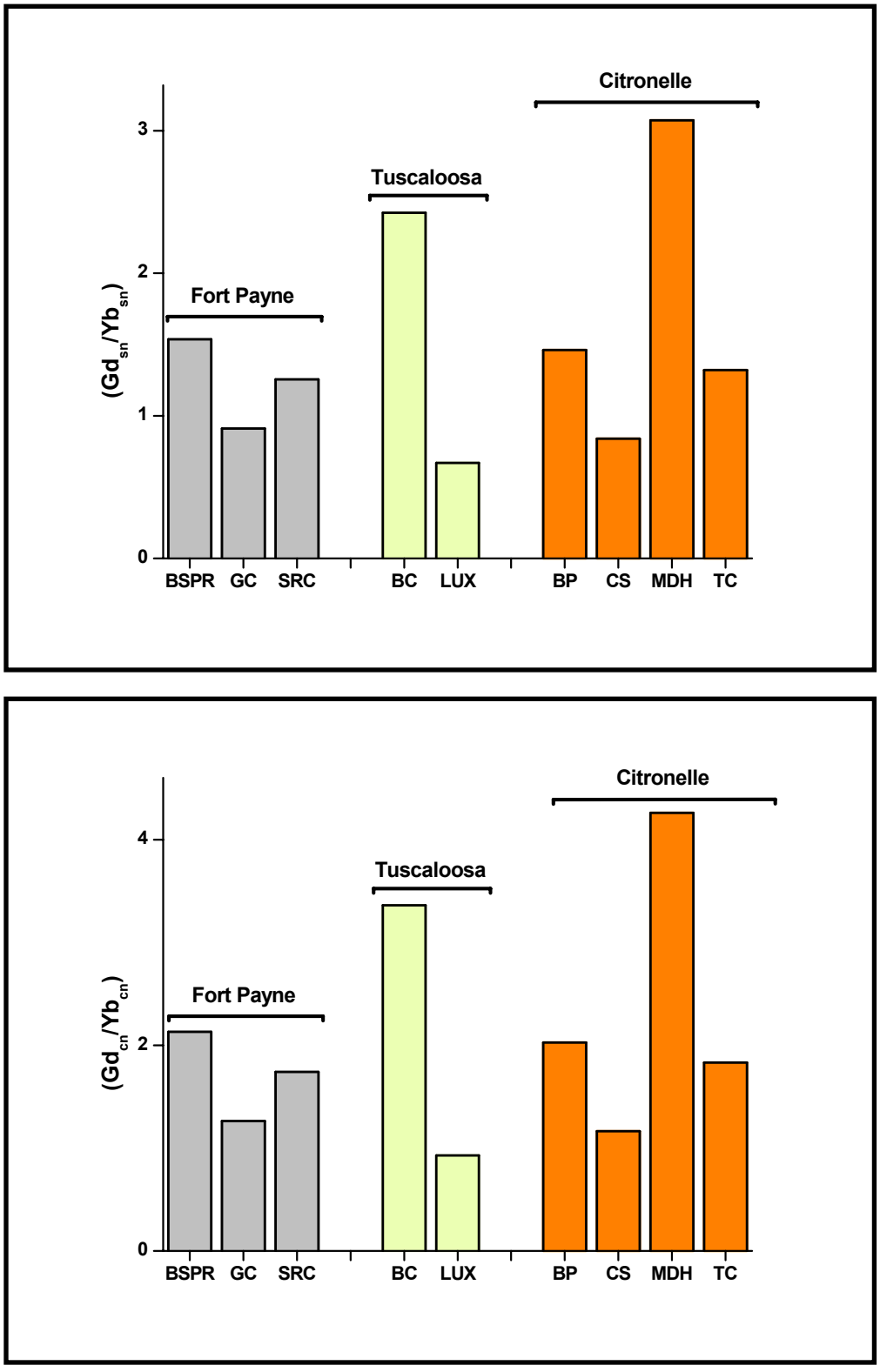


Fig. 2.11. Histograms of HREE depletions calculated from the sample means. Note the difference in scale between the two graphs.

Discussion

Three major trends emerge from the REE data. First, the Citronelle sample taken from Camp Shelby (CS) clusters with the samples taken from the Fort Payne Formation. Second, the Citronelle samples taken from Bayou Pierre (BP) and Topisaw Creek (TC) group together, and finally, the Citronelle sample taken at Mad Dog Hill (MDH) and the Tuscaloosa sample taken near Bear Creek (BC) both have high levels of HREE depletion. Based on these clusters, it seems that the Citronelle gravels in Mississippi were derived from at least two sources.

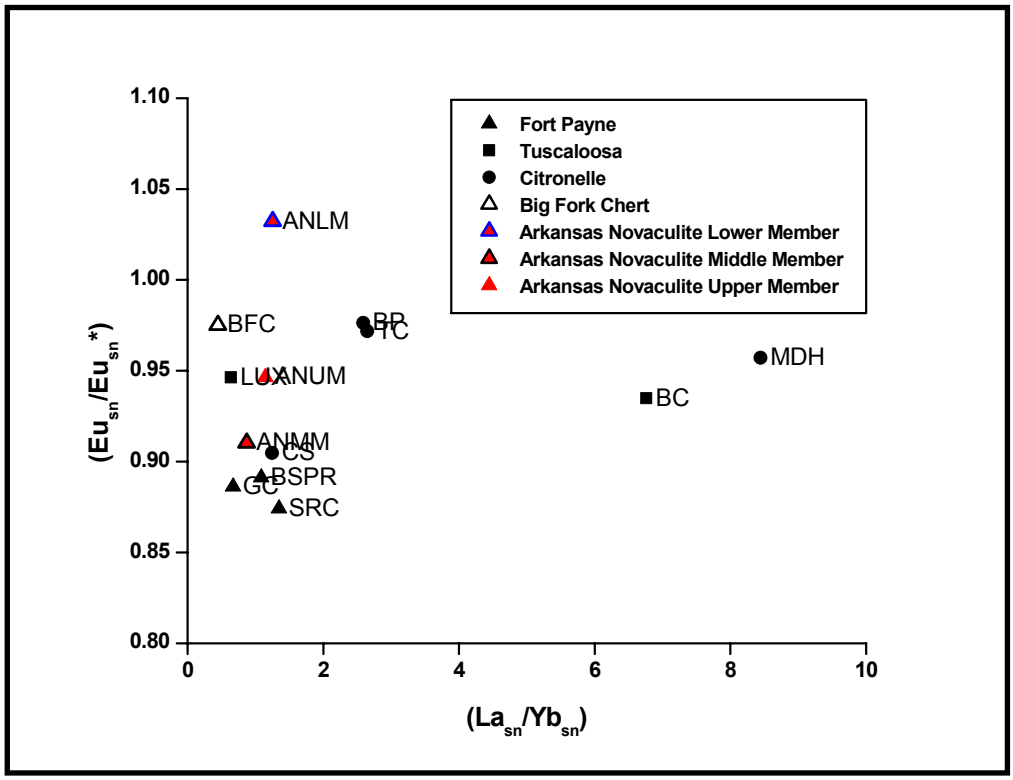
The grouping of the Camp Shelby sample with the Fort Payne Formation samples suggests that the Citronelle gravels in Pascagoula River basin were derived from the Fort Payne. It is unclear whether the source rock is from the formation in central Alabama or from the Highland Rim in Tennessee, but based on the amount of chert present in the Citronelle, it would seem that the Highland Rim is the more probable source, as the chert in the Fort Payne in central Alabama tends to occur as nodules formed in limestone and would not produce as much detrital chert as the in-situ bedded chert found on the Highland Rim. This finding is consistent with the hypothesis of Isphording (1983), who suggested that historically the Tennessee River continued through Sequatchie valley, across Alabama, and into the Pascagoula River basin of Mississippi (Fig. 2.4).

Samples of the Citronelle taken from Bayou Pierre and Topisaw Creek also group together, which indicates that they share a protolith, but they do not cluster with the Fort Payne Formation. This finding suggests that these two samples were not derived from the Highland Rim as would be expected based on the extra-basinal hypothesis of Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005). Bayou Pierre flows into the Mississippi River and Topisaw Creek is in the western Pearl River basin; however, Topisaw Creek is proximal to the divide between the Pearl and Mississippi River basins. It is possible that these Citronelle samples were transported from the upper Mississippi River valley as suggested by Potter (1955a, 1955b), from Crowley's Ridge in Arkansas as suggested by Guccione (1984), or from source rocks in the Ouachita or

Ozark Mountains and deposited by the ancestral Mississippi River as suggested by Russell (1987).

To further investigate the potential that the BP and TC samples were deposited by the Mississippi River, a REE dataset from the Ouachita Mountains was utilized. Reid (1994) analyzed the geochemistry and petrography of the Broken Bow uplift in southeastern Oklahoma and the resulting dataset includes REE signatures from the Ordovician-age Bigfork chert and the lower-upper members of the Devonian-age Arkansas novaculite. Reid (1994) utilized the Post-Archean average Australian shale (PAAS) values (Taylor and McLennan, 1988) to normalize the REE concentrations; therefore, to compare the REE signatures from the Arkansas Novaculite and Bigfork chert to the samples in this study, the REE concentrations for these samples were re-normalized and the Eu anomalies and LREE/HREE ratios were re-calculated following the methodology utilized for the samples collected for this study (Figs. 2.12 and 2.13).

Based on the inclusion of the data from the Bigfork chert and the Arkansas novaculite, the provenance of the BP and TC samples remains unclear, but based on the proximity of these samples to those from the Ouachitas, it suggests that the samples from Bayou Pierre and Topisaw creek were deposited by the ancestral Mississippi River, not the ancestral Tennessee. The inclusion of the Bigfork Chert and the Arkansas Novaculite data also renders the provenance of the Camp Shelby (CS) unclear as the middle member of the Arkansas Novaculite groups with the CS and Fort Payne samples. This finding suggests that the middle member of the Arkansas Novaculite and the Fort Payne were deposited in a similar environment, and seems to suggest that the Citronelle deposits in the Pascagoula basin could be derived from the Ouachitas; however, although the contribution of some material to the Citronelle by the Ouachitas should not be ruled out, Reid (1994) notes that the bedded chert in the middle member of the Arkansas Novaculite is typically less than 10 centimeters (cm) thick, and when compared to the 10 - 31 cm bedded Fort Payne chert of the Highland Rim (Marcher 1962), it seems unlikely that the middle member of the Arkansas novaculite could produce the amount of detrital chert found in the Citronelle.



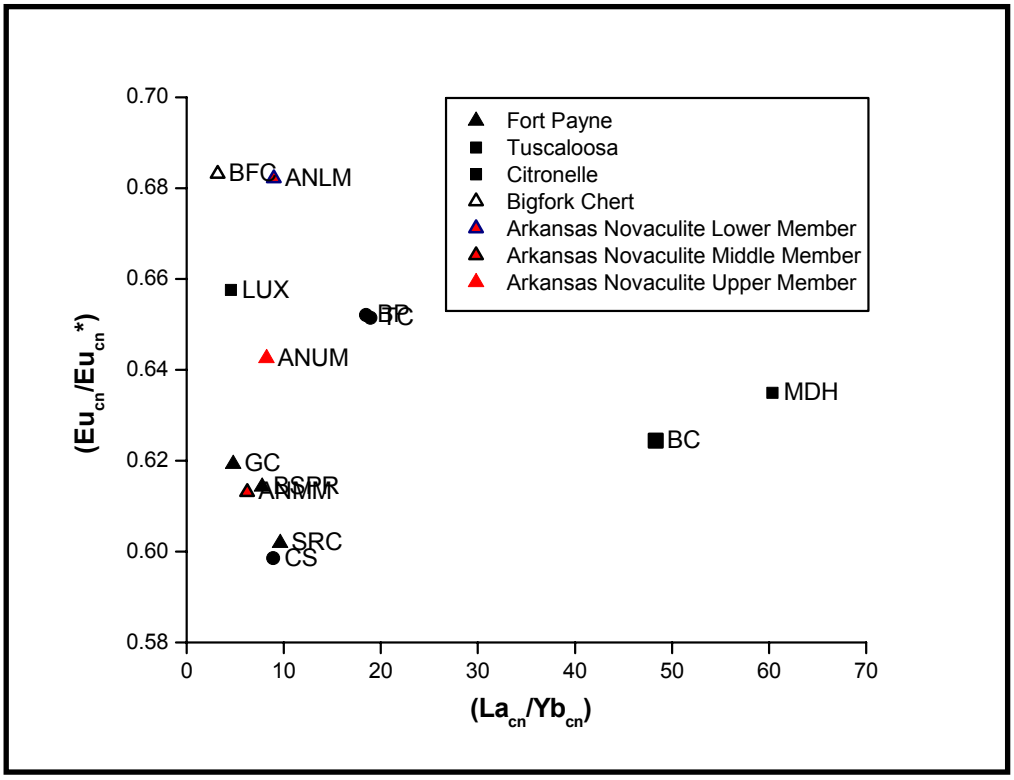


Fig. 2.12. Plots comparing the LREE/HREE ratio to the arithmetically derived Eu anomaly for both the samples used in this study and the Ouachita dataset of Reid (1994). Note the difference in scale between the two plots.

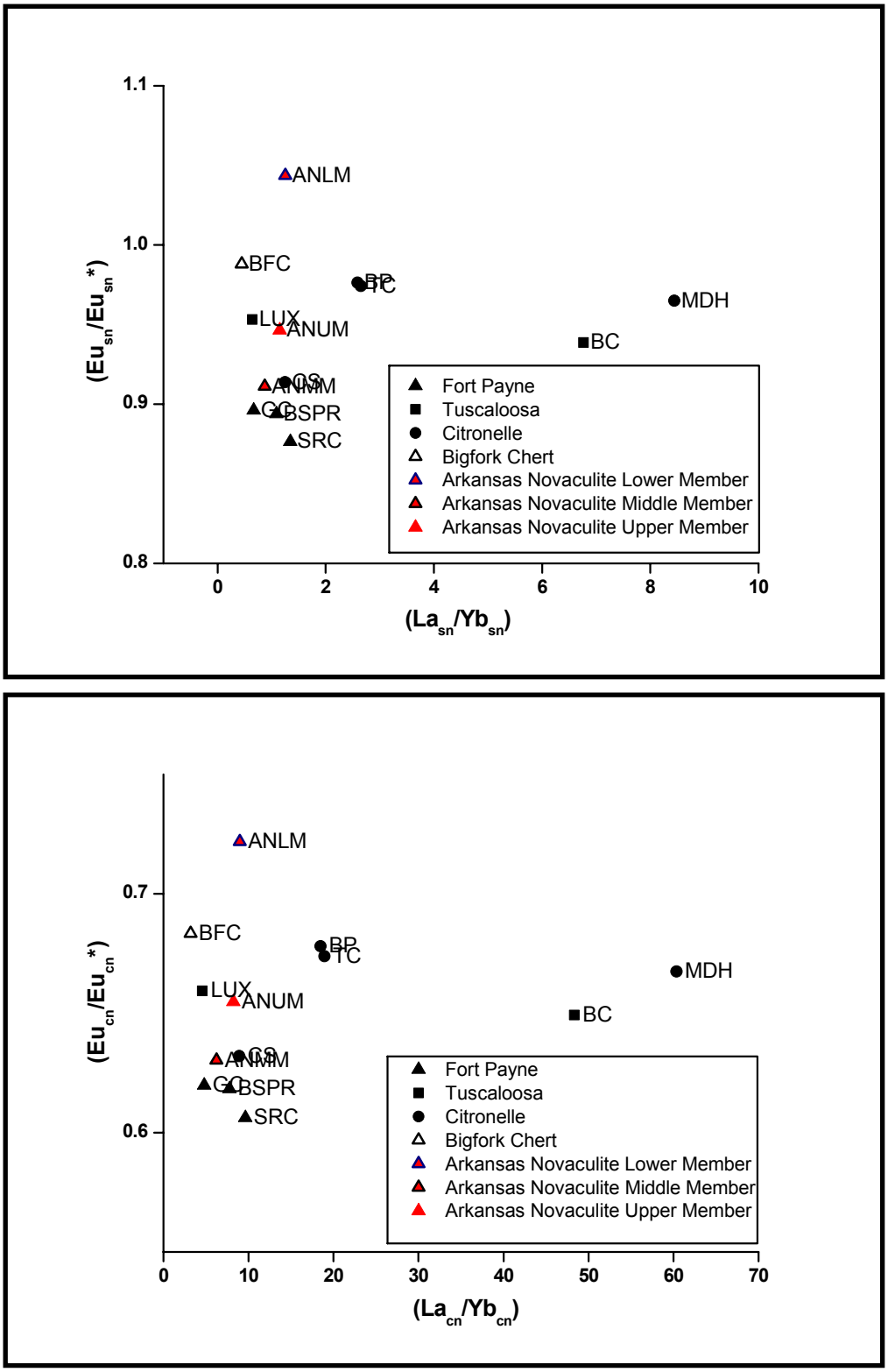


Fig. 2.13. Plots comparing the LREE/HREE ratio to the geometrically derived Eu anomaly for both the samples used in this study and the Ouachita dataset of Reid (1994). Note the difference in scale between the two plots.

Further, Reid (1994) notes that radiolarian fossils are noted from the middle member of the Arkansas Novaculite, but radiolarian fossils have not been recognized in the Citronelle Formation of Mississippi (Smith and Meylan 1983; Dockery 1996), which suggests that the CS sample was most likely derived from an Appalachian source.

Finally, the Bear Creek and Mad Dog Hill samples have similar REE behaviors and exhibit higher levels of HREE depletion, but this does not necessarily mean that these two samples share a protolith. As both samples are detrital, it is unclear where the source rock occurs. The similarity between the samples may be the result of localized perturbations that resulted in the HREE depletion. Cruse et al. (2000) found such a localized result in phosphate taken from samples of the Muncie Creek shale in Oklahoma and Kansas; however, the potential correlation of these samples should not be dismissed as the Tuscaloosa may be of Appalachian origin and could have been deposited by the ancestral upper Tennessee River.

Based on heavy mineral analyses, both Needham (1934) and Sayers and Udden (2010) have suggested that the Tuscaloosa Formation sediments were derived from the metamorphosed Inner Piedmont of the Appalachians, and Seifert and Chadima (1989) have shown that minerals exposed to metamorphism can exhibit HREE depletion. If the Bear Creek sample was derived from such an environment, it may explain the HREE depletion. Berry (1919), based on the deltaic nature of the Tuscaloosa, suggested that during the Cretaceous, the upper Tennessee River flowed into the Black Warrior River and was responsible for the deposition of the Tuscaloosa Formation, which would explain how the metamorphic minerals were transported to the Tuscaloosa. Similar minerals have been found in the Paleocene Midway and Eocene Wilcox Formations in Mississippi (Grim 1936). It is possible that the ancestral Tennessee as proposed by Berry (1919) extended into Mississippi depositing the Midway and Wilcox, and as sea level dropped, extended in a southerly course across the coastal plain entering the Gulf of Mexico through the lower Pearl River basin. Such a course would be somewhat analogous to the lower branch of the extra-basinal Tennessee River proposed by Combellas-Bigott and Galloway (2002,

2006) and Galloway (2005). An alternate explanation does however exist. Although the Fort Payne Formation is older than the Tuscaloosa, it was breached after deposition of the Tuscaloosa (Stearns and Reesman, 1986; Reesman and Stearns, 1989; Boettcher and Milliken, 1994; Combellas-Bigott and Galloway, 2002; Galloway, 2005; Combellas-Bigott and Galloway, 2006). If the breached Fort Payne material was being removed by the extra-basinal Tennessee River, its course would have cut across portions of the Tuscaloosa found in west-central Tennessee, ultimately reworking the Tuscaloosa and depositing materials from both formations in the lower Pearl River basin (Self, 1993).

Based on the trends in the REE data, the hypothesis that the Citronelle gravels in Mississippi were derived from the Fort Payne Formation can be partially accepted. The Citronelle gravels from the Pascagoula River basin exhibit REE behaviors similar to those from the Fort Payne Formation, and although the middle member of the Arkansas Novaculite groups with these samples, it seems unlikely that its thinly bedded chert could produce the quantity of detrital chert found in the Citronelle; however, the Citronelle samples taken from the lower Pearl River basin (MDH and TC) do not exhibit similar REE patterns. These findings suggest that the Citronelle is a multi-sourced deposit as suggested by Isphording (1976), May (1980), Self (1993), and May et al. (1995), and that the lower Pearl River basin may contain the remnants of at least two sources. This finding is not improbable if the systems carrying these materials were tributaries to the extra-basinal system proposed by Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005); however, caution must be used when correlating the Mad Dog Hill and Bear Creek samples. Although both exhibit similar REE behaviors, both are allocthtonous, and until a protolith is identified, the derivation of the Mad Dog Hill sample from the Tuscaloosa Formation will remain a hypothesis.

Conclusions

The results of the REE analysis suggest that, within Mississippi, the Citronelle may be a sedimentary "wastebasket" that contains the remnants of multiple formations transported by the ancestral Mississippi and Tennessee Rivers. These findings also suggest that the results of localized studies of the Citronelle should not be extrapolated to the entire formation due to the influence of different systems on different sections of the formation. The exact courses and natures of these systems, how long they persisted, and what happened to them remains unclear. The lack of information regarding the systems that deposited the Citronelle may also explain the age controversy because the systems that deposited the Citronelle may have existed at different times. Due to this potential temporal disparity, the timing of the different systems may only be constrained to post-Oliogocene as suggested by May (1980) and May et al. (1995). Some of these issues may be resolved if extensive mapping of the formation is undertaken (May et al. 1995) with the recognition that sections of the formation may have been deposited by different types of fluvial systems (i.e. non-braided streams) (Otvos, 2004). Further resolution may be gleaned from the mapping of the terraces along the Pascagoula River. With the exception of the mapping of the Alabama River terraces by Maxwell (1971) and the mapping of the Pearl River terraces by Cotten (1986), these types of studies are rare on the Gulf coastal plain. Also, REE data from the pre-loess/alluvial gravels along the Mississippi River, gravels from the upper Mississippi River valley, gravels from coeval packages in the Gulf, and cherts from the Ozark Mountains should also be collected and compared to the data from the Citronelle to further resolve issues related to its provenance.

Finally, the clustering of the middle member of the Arkansas Novaculite with the Citronelle sample from Camp Shelby and the Fort Payne samples exposes a caveat to using REE data alone to determine provenance. REE data tend to cluster based on deposition in similar environments, and if a source for the detrital materials under investigation is not suspected, the wrong conclusions may be reached. Murray (1994) has advocated using REE data in conjunction with

major and trace element data, and future geochemical studies of the Citronelle should incorporate such data. Geochemical data should also be considered along with published petrographic, mineralogic, and fossil analyses for a "total-evidence" package regarding the provenance of the detrital gravels of Mississippi.

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CHAPTER III

ICHTHYOLOGICAL INVESTIGATIONS INTO PALAEODRAINAGE HYPOTHESES FOR THE TENNESSEE RIVER: INSIGHTS FROM MOLECULAR PHYLOGENETIC ANALYSES AND BIOGEOGRAPHY OF THE *ETHEOSTOMA* SUBGENUS *DORATION* (TELEOSTEI: PERCIDAE)

Introduction

The recognition of a high level of species diversity in the Tennessee River basin is a result of numerous systematic studies of fishes found in the Tennessee River basin. These studies often contain the statuses, descriptions, and distributions of species within the Tennessee River basin, and many attempt to infer historical biogeographic patterns and the evolution of the species from their modern distributions (e.g., Page et al., 1992; Layman et al., 1993; Wood and Mayden, 1993; Wood, 1996; Ceas and Page, 1997; Wood and Mayden, 1997; Ceas and Burr, 2002; Porter et al., 2002; Page et al., 2003; Powers and Mayden, 2003; Burr et al., 2005; Powers and Mayden, 2007; Page and Near, 2007; Berendzen et al., 2008; Keck and Near, 2008; Layman and Mayden, 2009). Despite all of the biogeographic inferences, however, hypotheses regarding the drainage evolution of the Tennessee River are never directly tested (Starnes and Etnier, 1986), and the origin of its modern course remains enigmatic.

Beginning at the confluence of the Holston and Clinch Rivers in northeastern Tennessee, the Tennessee River begins a southward course towards Alabama. At Guntersville, Alabama, the Tennessee River makes an abrupt right angle turn to the west and begins flowing towards the Mississippi Embayment. As it reaches northeastern Mississippi, it once again makes a right angle turn sending it on a northward trending course. It flows north across Tennessee until it joins the Ohio River in Kentucky (Fig. 3.1) This circuitous route is of interest because determining how the river reached this course could provide valuable information on the evolution of both the basin itself and of the organisms that inhabit it (Starnes and Etnier, 1986).

Problems that confound understanding of the modern course of the Tennessee include difficulty in mapping the upper terraces of the river due to erosion or burial under extensive cover and a lack of readily identified remnant mapable channels. Despite these issues, numerous hypotheses have been proposed, though not rigorously tested, by both geologists and biologists to explain the course, and many of these hypotheses contain elements similar to those proposed by Hayes and Campbell (1894) in one of the first scientifically based explanations of the modern course of the Tennessee River.

Fig. 3.1. Map showing the modern course of the Tennessee River and other selected rivers.

Hayes and Campbell (1894) hypothesized that an Appalachian River system connected the upper Tennessee River basin to the Coosa River basin during the Cretaceous. Contemporaneously, the ancestral Sequatchie River connected to the Black Warrior River until the ancestral Sequatchie was captured by a stream occupying the same course as the modern

Tennessee across northern Alabama (Fig. 3.2). Throughout the early Tertiary, the pirated ancestral Sequatchie followed the course of the Big Black River towards the Mississippi Embayment. During the late Tertiary, progressive headcutting into Walden Plateau by both the ancestral Sequatchie and the Appalachian Rivers led to the formation of Walden Gorge. The Appalachian River was then diverted through Walden Gorge and captured by the ancestral Sequatchie due to its lower elevation. The ancestral Sequatchie then continued its path towards the embayment until a cycle of uplift allowed a northwestward flowing stream headcut into the ancestral Sequatchie in northeastern Mississippi, separating the Big Black and ancestral Sequatchie River systems, and establishing the modern course of the Tennessee River (Fig. 3.3). Subsequently, geologists such as White (1904), Johnson (1905), and Adams (1928) noted that structural and stratigraphic evidence supporting the hypotheses of Hayes and Campbell (1894) was lacking, and suggested that the course of the Tennessee River had been established by the Cretaceous.

Fig. 3.2. Approximation of the Cretaceous course of the ancestral Sequatchie and Appalachian Rivers of Hayes and Campbell (1894). Modified from Hayes and Campbell (1894) and Johnson (1905).

Fig. 3.3. Course of the Tertiary Tennessee River. Modified from Chamberlin and Salisbury (1905).

Shaw (1918), further noting that many of the details surrounding the history of the Tennessee River as outlined by Hayes and Campbell (1894) needed modification, argued that the Tennessee River never utilized the Big Black River in a course towards the Mississippi Embayment. Shaw (1918) based his argument on the lack of high terraces along the Big Black River and the lack of an abandoned river valley between the Big Black and the Tennessee River systems. Instead, Shaw (1918) hypothesized that during the Pliocene, the headwaters of the Big Black River were captured from the Pearl River. This hypothesis was based on three lines of evidence. First, rather than continuing in a westerly course towards the Mississippi River, the Pearl River makes an anomalous southward turn at Jackson, Mississippi, but its main tributaries are east of the river, suggesting that the Pearl had tributaries to the west which have been captured. Second, Shaw (1918) argued that although the Pearl River channel is 50-100 feet higher than the channel of the

Big Black River, small southern tributaries in the Big Black system are pushing the divide closer to the Pearl River. Lastly, Shaw (1918) noted that the lower Pearl River is a misfit stream as the modern Pearl is too small to have incised the course in which it now flows.

Shaw (1918) hypothesized that during the Pliocene, the ancestral Tennessee flowed through the Tombigbee River valley. This hypothesis was based on: (1) the proximity of the headwaters of the Tombigbee River to the Tennessee River and (2) the flow of the Tennessee River across a rocky shoal found in a narrow valley near Iuka, Mississippi. Shaw (1918), however, notes that no remnant courses of this system have been recognized.

A recent comprehensive analysis of available geological data by Galloway (2005) and Combellas-Bigott and Galloway (2006) suggests that from the Miocene to the Pliocene, an extra-basinal fluvial system, the ancestral Tennessee River, flowed across the state of Mississippi. The extra-basinal Tennessee River system was initiated in response to the breaching of the Nashville Dome and had three westward flowing branches, one flanking the northern edge of the Nashville dome, one flanking the southern edge of the dome, and one draining the southern Appalachians in a course that approximates the upper Coosa and Black Warrior River systems. These branches flowed into the mainstem ancestral Tennessee River that crossed the state of Mississippi. The ancestral Tennessee then directly entered the Gulf of Mexico in a course that approximates the course of the modern lower Pearl River (Fig. 3.4).

Despite the lack of geological evidence, the Appalachian River hypothesis of Hayes and Campbell (1894) has become ingrained in the biological literature. This paradox has been termed the "Coosa problem" by Deevey (1949) and has largely arisen from observed faunal affinities between aquatic organisms in the upper Tennessee River and the Coosa River (e.g. Simpson, 1900; Adams, 1901; Adams, 1902; Ortmann, 1905; van der Schalie, 1938; Ross, 1952, 1971; Wiley and Mayden, 1985; Swift et al., 1986; Starnes and Etnier, 1986; Mayden, 1988; Wood, 1996; Near, 2002; Berendzen et al., 2003; Ghedotti et al., 2004). Recently, Kozak et al. (2006) found that haplotype divergence within salamanders of the *Eurycea bislineata* species complex

supported the existence of two independent Pliocene drainages that eventually merged to form the modern Tennessee River. The course of one of the independent drainages inferred by Kozak et al. (2006) closely approximates the course of the Appalachian River of Hayes and Campbell (1894); however, the course of the other independent drainage follows the course of the Cumberland River into what is the modern Mississippi River.

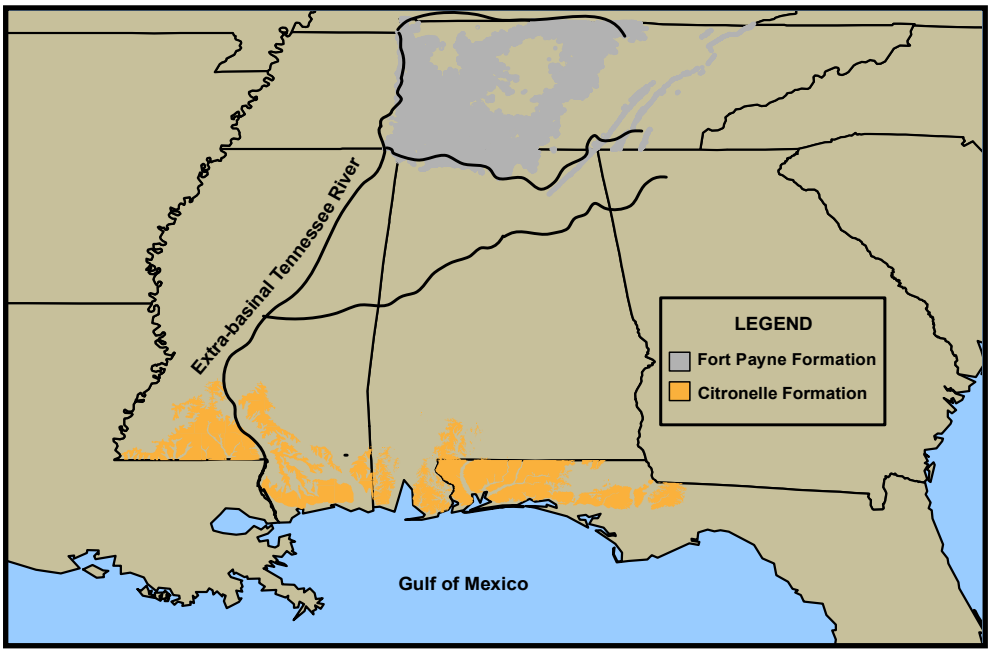

Fig. 3.4. Extra-basinal Tennessee River system. Modified from Galloway (2005) and Combellas-Bigott and Galloway (2006).

Alternative hypotheses regarding the evolution of the Tennessee River, such as the course of the ancestral Sequatchie River of Hayes and Campbell (1894) and the extra-basinal fluvial system of Galloway (2005), have largely been ignored in the biological literature due to a paucity of information regarding the phylogenetic relationships of aquatic organisms distributed along Gulf of Mexico coastal plain (Fitzpatrick, 1986; Starnes and Etnier, 1986; Layman, 1994). For this study, a phylogenetic analysis of the *Etheostoma stigmaeum* species complex, which is widespread throughout the region under investigation, will be used to test the following

respective hypotheses of Hayes and Campbell (1894) and Galloway (2005) regarding the evolution of the lower Tennessee River: (1) the ancestral Sequatchie River flowed towards the Mississippi Embayment by following the course of the modern Big Black River across Mississippi, and (2) the ancestral Tennessee River flowed across Mississippi with an outlet to the Gulf of Mexico via the modern lower Pearl River.

Phylogenetic relationships among fishes have been used to provide evidence for ancestral river systems. For example, Berendzen et al. (2003) found that relationships among the Cypriniform genus *Hypentelium* supported the location and existence of the ancient Teays River system. Geological evidence for the Teays River valley has long been recognized, and the valley itself has been mapped (Melhorn and Kempton, 1991), but as few remnant channels of the ancestral Tennessee River exist to be mapped, hypotheses must be tested by other means such as the use of organismal proxies.

Previous Studies of the *Etheostoma stigmaeum* Species Complex

Subgeneric Level Studies

Initially, the subgenus *Doration*, which contains the *Etheostoma stigmaeum* species complex, was placed in the subgenus *Boleosoma*, and this subgenus was inclusive of *Etheostoma chlorosoma* (Bailey and Gosline, 1955). A revision by Cole (1967) moved *Etheostoma chlorosoma* to the subgenus *Vaillantia*, and *Etheostoma stigmaeum* and *Etheostoma jessiae* were assigned to *Doration*. Howell (1968) considered *Doration* as intermediate between the subgenera *Vaillantia* and *Oligocephalus* but believed *Doration* to be more closely allied with the latter due to a natural hybridization event between *Etheostoma (Doration) stigmaeum* and *Etheostoma (Oligocephalus) artesiae* (Howell and Boschung, 1966). Confusion on the subgeneric placement of *Doration* continued when Bailey and Etnier (1988) assigned the subgenus to a complex inclusive of the *Boleosoma*, *Vaillantia*, and *Ioa* subgenera, and in a subsequent analysis of allozyme data by Wood and Mayden (1997), similar results were recovered. Simon (1994) recovered a monophyletic *Doration* based on the early life histories of *Etheostoma stigmaeum*

and *Etheostoma jessiae*. Analysis of the mitochondrial cytochrome *b* and 12S rRNA genes by Sloss et al. (2004) recovered *Etheostoma (Doration) stigmaeum* and *Etheostoma (Vaillantia) chlorosoma* as sister species. This relationship was also supported by Mayden et al. (2006) who, based on mitochondrial cytochrome *b* sequences, recovered a monophyletic clade that placed *Doration* and *Vaillantia* as sister subgenera. Based on morphological similarities, Cook (1959) noted the close relationship between *Doration* and *Vaillantia* some 45 years earlier. This relationship has been further supported with sequence data generated from the mitochondrial ND2 and nuclear S7 genes (Lang and Mayden; 2007).

Species Level Studies

The *Etheostoma stigmaeum* species complex consists of the described species *Etheostoma stigmaeum* (Jordan 1877), *Etheostoma jessiae* (Jordan and Brayton 1878), *Etheostoma meadiae* (Jordan and Evermann 1898), and *Etheostoma akatulo* Layman and Mayden 2009. In addition, based on standard measurements, meristics, breeding colors, and allozyme differentiation, Layman (1994) recognized five additional species that still lack formal description: *Etheostoma* sp. beaded darter, *Etheostoma* sp. highland darter, *Etheostoma* sp. bluegrass darter, *Etheostoma* sp. clown darter, and *Etheostoma* sp. longhunt darter. Simon (1994) recognized a unique entity, *Etheostoma stigmaeum ozarcanus*, from the Caddo River of Arkansas and considered this subspecies to be present throughout Kansas, Missouri, Oklahoma, and Arkansas; therefore, based on its distribution, it would be synonymous with both the *E.* sp. beaded darter and *E.* sp. highland darter of Layman (1994), but this subspecies also lacks formal description. Due to the potential confusion over the synonymy in the species found west of the Mississippi, the species nomenclature utilized by Layman (1994) will be followed where the nine total species from the complex form a monophyletic group.

Species Accounts

Etheostoma stigmaeum (Jordan) Species Complex

Speckled Darter

Synonymies: Species synonyms are given in Layman (1994).

Distribution: *Etheostoma stigmaeum* is found in the Conecuh, Escambia, and Perdido Bay drainages of Florida and Alabama, and the Blackwater drainage of Florida. In Alabama, *Etheostoma stigmaeum* is distributed in the Tennessee (Bear Creek only), Tombigbee, Black Warrior, Alabama, Cahaba, Coosa, and Tallapoosa drainage systems. From the Coosa drainage, the range extends into northwestern Georgia and includes the Etowah and Conasauga River drainages. *Etheostoma stigmaeum* is distributed in the Pascagoula, Pearl, Amite, Homochitto, Bayou Pierre, Big Black, Yazoo, Hatchie, Tombigbee, and Tennessee drainages of Mississippi. The range extends west into the Lake Pontchartrain-Maurepas, Red-Ouachita, and Sabine River systems of Louisiana. *Etheostoma stigmaeum* is also found in the Neosho, Red-Ouachita and Arkansas River systems of Oklahoma, Kansas, Missouri and Arkansas. In Tennessee, the range includes the Hatchie, Tennessee, Duck, and Cumberland River systems. The northern limits of the range include the Green and Barren River systems of the Ohio drainage in Kentucky (Table 3.1; Fig. 3.5) (Jordan, 1877; Blair, 1959; Cook, 1959; Howell, 1968; Douglas, 1974; Clay, 1975; Robison and Buchanan, 1988; Etnier and Starnes, 1993; Jenkins and Burkhead, 1993; Cross and Collins, 1995; Pflieger, 1997; Ross, 2001; Boschung and Mayden, 2004; Miller and Robison, 2004; Skelton and Albanese, 2006).

Layman (1994) recognized five additional species from the broadly circumscribed *Etheostoma stigmaeum* that still lack formal description. These include *Etheostoma* sp. clown darter, which is endemic to the Buffalo and Duck Rivers of the Tennessee drainage basin in Tennessee, *Etheostoma* sp. longhunt darter, which is endemic to the Rockcastle and Red River drainages of the Cumberland drainage basin in Kentucky and northern Tennessee, *Etheostoma* sp. bluegrass

darter, which is endemic to Barren and Green Rivers of the Ohio River drainage in Kentucky, *Etheostoma* sp. highland darter which is endemic to the White and Arkansas River drainages of Kansas, Oklahoma, Missouri, and Arkansas, and *Etheostoma* sp. beaded darter, which is endemic upper Caddo and Upper Ouachita Rivers of Arkansas.

Table 3.1

Distributions of the Etheostoma stigmaeum *Species Complex Summarized from Layman (1994) and Simon (1994)*

Species	Distribution
Etheostoma stigmaeum	-Mobile Basin -Drainages of Mississippi exclusive of those in the Delta -Gulf Coast drainages of Louisiana -Flanks of the Mississippi Embayment in Arkansas and Missouri -Bear Creek, Alabama (tributary to the Tennessee River)
Etheostoma jessiae	-Endemic to tributaries of the Tennessee River exclusive of the Duck River
Etheostoma meadiae	-Endemic to the Clinch and Powell Rivers above Norris Dam
Etheostoma akatulo	-Endemic to Caney Fork River (tributary to the Cumberland River)
E. sp. clown darter	-Endemic to the Buffalo and Duck Rivers of Tennessee
E. sp. longhunt darter	-Endemic to the Rockcastle and Red Rivers of the Cumberland River drainage
E. sp. bluegrass darter	-Endemic to the Barren and Green Rivers of Kentucky and Tennessee
E. sp. highland darter	-Endemic to the White and Arkansas River drainages of the Ozark Plateau
E. sp. beaded darter	-Endemic to the upper Caddo and Upper Ouachita Rivers

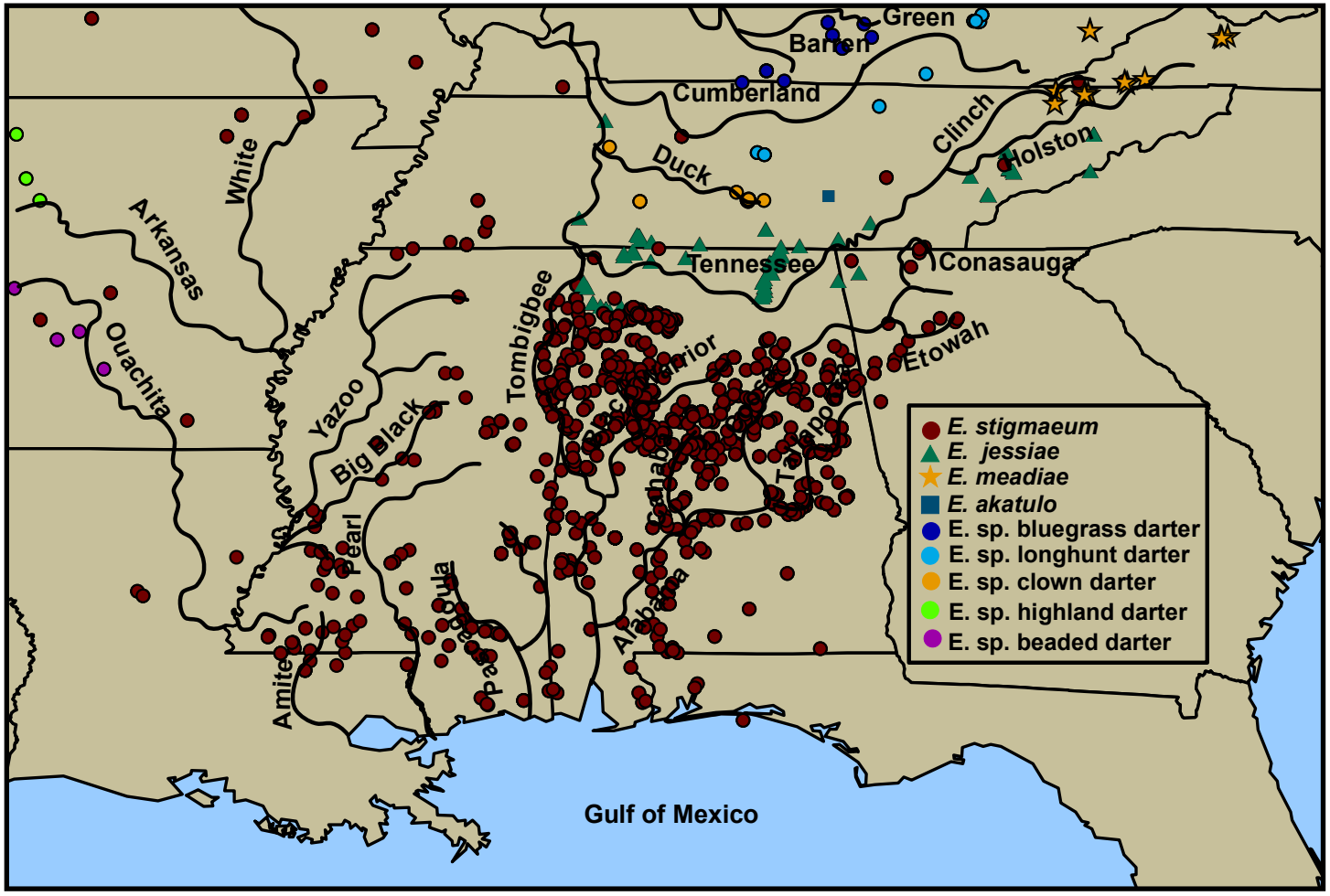

Fig. 3.5. Distribution of Doration within Mississippi, Alabama, and Mississippi. Map is based on collection data from the University of Alabama Ichthyological Collection, the Mississippi Museum of Natural Science, Ross (2001), and the collection data from the author.

Habitat: *Etheostoma stigmaeum* is found over sand and gravel substrates in the pools and riffles of streams with moderate flow (Boschung and Mayden, 2004).

Life History: Mating occurs between March and May over gravel substrates. Males position themselves on the backs of the females and vigorously vibrate until both the pair and the eggs are buried in the substrate. Following mating, the male will defend the territory, but will only attack other speckled darters (Winn, 1958a; Winn, 1958b; Page et al., 1982; Hubbs, 1985). Speckled darters hatch at total lengths (TL) ranging from 4.6 to 5.4 mm (Simon, 1997). Layman (1994) reported a maximum standard length of 51.8 mm for adult males from the Green River and a maximum standard length (SL) of 42.0 mm for adult females from the Coosa River.

Etheostoma jessiae (Jordan and Brayton)

Blueside Darter

Synonymies: Species synonyms are given in Layman (1994).

Distribution: *Etheostoma jessiae* is distributed in the North Fork of the Holston River in Virginia, and the Clinch, Powell, and Tennessee Rivers of Tennessee exclusive of the Duck River. The blueside darter also occurs in the Tennessee drainage of Alabama and the Mills Creek system of North Carolina (Table 3.1; Fig. 3.5) (Howell, 1968; Jenkins and Burkhead, 1993; Layman, 1994; Rohde et al., 1994).

Habitat: *Etheostoma jessiae* is found in pools and riffles with sand and gravel substrates in creeks and small rivers with a moderate to swift current (Boschung and Mayden, 2004).

Life History: A female will enter a spawning site and be pursued by a male who will mount her when the appropriate substrate is reached. Based on aquarium observations, eggs are deposited in gravel substrates. In Tennessee, blueside darters hatch at a TL ranging from 5.3 to 6.0 mm (Simon, 1997). Males attain a maximum SL of 57.7 mm, while females are slightly smaller reaching a maximum SL of 51.7 (Layman, 1994).

Etheostoma meadiae (Jordan and Evermann)

Bluespar Darter

Synonymies: Species synonyms are given in Layman (1994).

Distribution: *Etheostoma meadiae* is endemic to the Clinch and Powell River drainages of Virginia and Tennessee (Fig. 3.1) (Jenkins and Burkhead, 1993; Layman, 1994). Some have argued that *Etheostoma meadiae* is the result of an introgression between *Etheostoma stigmaeum* and *Etheostoma jessiae* and should have subspecies status as *Etheostoma stigmaeum meadiae* (Starnes and Etnier, 1986; Jenkins and Burkhead, 1993; Layman, 1994). Layman (1994) chose to recognize it as a distinct entity based on morphological and breeding color characteristics.

Habitat: *Etheostoma meadiae* is found over sand to boulder-sized substrates in the riffles and pools of small to moderate sized creeks with moderate to swift currents (Howell, 1980).

Life History: Based on the timing of males in breeding color, spawning may occur between March and April. Reproductive behavior is assumed to be similar to that of *Etheostoma stigmaeum* (Howell, 1980).

Etheostoma akatulo (Layman and Mayden)

Bluemask Darter

Synonyms: This entity was first recognized as *Etheostoma stigmaeum parvigemma*, the gem darter, by Howell (1968), but a formal description was never published. Subsequently, the common name of jewel darter became attached to this species (Biggins, 1993) until Layman (1994) assigned it the common name of bluemask darter. Layman and Mayden (2009) have provided a formal description naming it *Etheostoma akatulo*, the bluemask darter, thus elevating it to species status. Other synonymies are given in Layman (1994).

Distribution: The bluemask darter is endemic to the Collins, Rocky, Cane Creek, and Caney Fork River systems of the Cumberland River drainage in Tennessee (Fig. 3.1) (Layman et al., 1993; Layman and Mayden, 2009). Historically, this species was found in the Calfkiller River of the Cumberland drainage (Howell, 1968), but in a subsequent survey of the Calfkiller River,

bluemask darters were not collected, and it is believed that *Etheostoma akatulo* has been extirpated from the Calfkiller (Layman et al., 1993). Unfortunately, the remaining populations of bluemask darters are isolated from one another by the Great Falls Reservoir which has resulted in low gene flow among the populations and inbreeding depression within the populations (Smith, 2005). Based on its endemicity and anthropogenic threats to its habitat, the bluemask darter is listed as federally endangered by the United States Fish and Wildlife Service (Biggins, 1993).

Habitat: The bluemask darter is found in 10 to 50 cm of water covering sand and gravel substrates at the edges of pools, downstream of riffles, and in runs in small rivers with slow to moderate currents (Layman et al., 1993).

Life History: Spawning behavior is similar to that of the other members of *Doration*. The bluemask darter spawns in water temperatures between 16.5 and 23.5° C. Females swim into the spawning area, where, facing upstream, one male mounts the female and they simultaneously vibrate until both the ventral surface of the female and the eggs are buried in the sand. The same pair may spawn several times, and the male will aggressively defend the female until she is no longer receptive to spawning behavior (Simmons and Layzer, 2004). Adult males attain a maximum standard length of 57.7 mm, while females attain a maximum standard length of 51.7 mm (Layman and Mayden, 2009).

Hypotheses Testing and Expected Results

In order to test the drainage hypotheses of Hayes and Campbell (1894) and Galloway (2005), phylogenetic systematics of the *Etheostoma stigmaeum* species complex were used to infer relationships of both the species themselves and of populations within the species complex. Most phylogenetic studies are performed to assess the relationships, character evolution, and the potential for the presence of cryptic species within the group under investigation. Secondary to these goals is the biogeographical inference of ancestral drainage patterns based on the results of the phylogenetic analyses. With respect to the drainage hypotheses under investigation, if the drainage hypothesis of Hayes and Campbell (1894) is supported by phylogenetic relationships,

fishes collected from the lower Bear Creek system of Alabama and Mississippi of the lower Tennessee River valley will be most closely related to those collected in the Yazoo, Big Black, and Bayou Pierre systems of the Mississippi River basin of Mississippi. Conversely, if the drainage hypothesis of Galloway (2005) is supported, phylogenetic relationships should infer that fishes collected from the Buffalo/Duck River system of the western Highland Rim, fishes from the lower Bear Creek system of the lower Tennessee River valley, and fishes from the Black Warrior River basin will be most closely related to those collected in the Pearl River basin of Mississippi; however, these hypotheses are contingent on the assumption that few, if any, drainage extinctions have occurred and that the break-up of these drainage systems coincides with species evolution and subsequent accumulation of synapomorphic DNA mutations within the drainages.

Materials and Methods

The research protocol utilized in this study was submitted to and approved by the University of Southern Mississippi Institutional Animal Care and Use Committee (approval number 10052401; Appendix B). To test the drainage hypotheses that place the course of the ancestral Tennessee River across Mississippi, members of *Doration* were either collected under the appropriate permits using a seine or were donated (Appendix C). All specimens used for molecular analysis were preserved in 95% ethanol. Voucher specimens were initially preserved in 10% formalin, and after 48 hours, they were soaked in water for 72 hours and then transferred to 70% ethanol for reposition. Voucher specimens were deposited in the Mississippi Museum of Natural Science Ichthyology Collection in Jackson, Mississippi (Appendix C).

DNA Extraction and Sequencing

Fin clips were taken from the caudal, pectoral, pelvic, or anal fins of the fishes preserved in 95% ethanol, and the DNeasy® Blood and Tissue Kit (Qiagen Sciences, Maryland) was used to extract whole genomic DNA from these clips. When available, DNA was extracted from at least

three fishes per drainage. The mitochondrial cytochrome *b* (cyt *b*) gene, NADH subunit 5 (ND5) gene, and the nuclear S7 gene were amplified by polymerase chain reaction (PCR) using 18µl of sterile water, 25µl of Takara Ex Taq™ Polymerase, which is premixed with 0.05 U/µL of enzyme and a dNTP concentration of 0.4 mM per nucleotide (TaKaRa Bio USA, Madison, Wisconsin), 2.5 µl of the forward primer, 2.5 µl of the reverse primer, and 2 µl of the extracted DNA.

PCR products were electrophoresed on a 1% agarose gel, soaked in ethidium bromide diluted with sterile water for 20 minutes, and placed on an ultraviolet light box to check for the presence of bands corresponding to the length of the gene that was amplified. PCR products containing amplicons of the appropriate lengths were purified using the QIAquick® PCR Purification Kit (Qiagen Sciences, Maryland), and their DNA concentrations were measured on a NanoDrop® ND 1000 spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts). Products with peaks at 260 nm were sent to Eurofins MWG Operon (Huntsville, Alabama) for sequencing.

Sequence Alignment, Phylogenetic Analysis, and Divergence Estimations

Forward and reverse sequences were assembled using Sequencher 4.7 (GeneCodes Corporation, Ann Arbor, Michigan), and ambiguities were assessed and resolved by eye. A complete alignment of the sequences was performed with the default multiple alignment mode in ClustalX (Thompson et al., 1997), and the alignments were verified by eye. WinClada v.1.00.08 (Nixon, 2002) was used to perform a heuristic parsimonious search of tree space with the values of 5000 maximum trees to keep, 500 replications, and 5 starting trees per replication using an unconstrained multi-tree bi-section reconnection (TBR) option to search for the most parsimonious tree. Bootstrap replicates were set at 1000, with 10 search repetitions per replicate, and 2 saved trees per repetition. The node frequencies from the bootstrap analyses were calculated for the strict-consensus tree. Based on the broader findings of Sloss et al. (2004), Mayden et al. (2006), and Lang and Mayden (2007), all trees were rooted with *Etheostoma (Vaillantia) chlorosoma*. Following phylogenetic analysis, uncorrected *p*-distances within

Doration were estimated for each gene using MEGA (Molecular Evolutionary Genetic Analysis) 4.0 (Tamura et al., 2007).

Mitochondrial Cytochrome b *Gene*

The ~1140 base pair (bp) mitochondrial cytochrome *b* (cyt *b*) gene was amplified using the L14724 and H15915 primers of Schmidt and Gold (1993) or either the L14724 primer of Schmidt and Gold (1993) and the H15918R primer of Song et al. (1998) (Table 3.2). The thermal cycling profile included an initial step of 94°C for 3 minutes, followed by 30 cycles of denaturing at 94°C for 30 seconds, annealing at 55°C for 30 seconds, and extension at 72°C for 1 minute 10 seconds. A final extension of 72°C for 5 minutes was followed by a holding temperature of 4°C.

Mitochondrial NADH Subunit 5 (ND5) Gene

The ~720 bp ND5 gene was amplified using the ND5F_stig and ND5R_stig primers designed for this study (Table 3.3). The thermal cycling profile was modified from the ND2 amplification protocol of Lang and Mayden (2007) and included an initial step of 94°C for 3 minutes, followed by 35 cycles of denaturing at 94°C for 40 seconds, annealing at 60°C for 60 seconds, and extension at 72° for 1 minute 30 seconds. A final extension of 72°C for 5 minutes was followed by a holding temperature of 4°C.

Table 3.2

Primers Used to Amplify the Genes Used in This Study

Gene	Primer	5'-3' Sequence	Reference
Cyt *b*	L14724	GTGACTTGAAAAACCACCGTTG	Schmidt and Gold (1993)
Cyt *b*	H15915	CAACGATCTCCGGTTTACAAGAC	Schmidt and Gold (1993)
Cyt *b*	H15918R	CTCCATCTCCGGTTTACAAGAC	Song et al. (1998)
ND5	ND5F_stig	GCAAACACNGCNGCCCTYCAAGC*	
ND5	ND5R_stig	GCTCAGGCGTTTAGRTGGGATGTG*	
S7	S7RPEX1F	TGGCCTCTTCCTTGGCCGTC	Chow and Hazama (1998)
S7	S7RPEX2R	AACTCGTCTGGCTTTTCGCC	Chow and Hazama (1998)
S7	S7EtheosR	CGCCATTAGGCTTCACTATT*	

Note. * Designed specifically for this study.

First Intron of the Nuclear S7 Ribosomal Protein

The ~523 bp first intron of the nuclear S7 ribosomal protein was amplified using the S7RPEX1F and S7RPEX2R primers of Chow and Hazama (1998) (Table 3.3). Amplification was achieved using the stepped thermal cycling profile developed by Piller et al. (2008) whereby an initial denaturation step of 94°C for 2 minutes is followed by 29 cycles at 94°C for 2 minutes. The stepped annealing profile then begins with 2 cycles at 62°C for 30 seconds followed by 2 cycles at 61°C for 30 seconds, 4 cycles at 59°C for 30 seconds, and ends with 21 cycles at 58°C for 30 seconds. Each cycle has a 1 minute extension step at 72°C. The cycling ends with a final extension at 72°C for 4 minutes followed by a holding temperature of 4°C.

Results

All samples were not sequenced for all loci due to amplification problems that may have resulted from base mismatches between the primers and the sample or the presence of inhibitors in the extracted DNA. Further, the nuclear S7 gene was sequenced for thirty-four individuals, but analyses of those preliminary data yielded little variation providing no phylogenetic resolution and were not continued for the remaining samples.

Cyt b *Gene*

Eighty-seven samples were included in the phylogenetic analysis of the cyt *b* gene. The aligned cyt *b* dataset consisted of 1179 bases, 739 of which were non-informative, leaving 440 parsimony informative (PI) characters. The heuristic search returned 920 equally most parsimonious trees (MPTs) with a length (L) of 2898, a consistency index (CI) of 0.27, and a retention index (RI) of 0.61. Twenty-five nodes were collapsed on the strict-consensus tree (Fig. 3.6).

Based on the topology inferred from the analysis of the cyt *b* gene, *Doration* forms a monophyletic group with *Etheostoma meadiae* recovered as sister to all remaining members of *Doration*. *Etheostoma akatulo* is recovered as sister to *Etheostoma jessiae*, the undescribed *Etheostoma* spp., and the nominal *Etheostoma stigmaeum*. The bluegrass, clown, and longhunt

darters form a paraphyletic group to *Etheostoma jessiae,* but the clown darter is recovered as non-monophyletic. The paraphyletic group plus *Etheostoma jessiae* is sister to the remaining *Doration*, which can be broadly divided into six well-supported clades.

1. Eastern Mississippi River Clade – The eastern Mississippi River clade consists of *Etheostoma stigmaeum* from the Yazoo, Big Black, Bayou Pierre, and Homochitto systems of Mississippi. Each of these systems drains directly into the Mississippi River. Internally, the Yazoo is recovered as sister to both the Big Black and Bayou Pierre systems, and this relationship is well supported. Mean intraclade divergence is 0.0091.

2. Western Mississippi River Clade – This clade is composed of the beaded and highland darters which occur respectively in the Caddo-Ouachita and White-Arkansas drainages that ultimately drain into the Mississippi River. The beaded darter is recovered as sister to the highland darter. Relationships within this clade are well-supported. Mean intraclade divergence is 0.0062.

3. Coosa Clade – This well-supported clade consists of *Etheostoma stigmaeum* from the Coosa River basin including the Conasauga River and Little Canoe Creek, both of which are tributaries to the Coosa River. The Conasauga sample is recovered as sister to the Little Canoe Creek samples. Mean intraclade divergence is 0.0041.

4. Tennessee-Tombigbee (Tenn-Tom) Clade – The Tenn-Tom clade consists of the Bear Creek from the lower Tennessee River drainage and the major tributaries to the Tombigbee River. Within this larger clade, a well-supported monophyletic Black Warrior River clade is recovered. The Black Warrior clade is sister to the remaining Tombigbee tributaries and Bear Creek. Minor structure exists between the remaining Tombigbee tributaries and Bear Creek. Mean intraclade divergence is 0.0087.

5. Alabama Coastal Plain Clade – The Alabama Coastal Plain clade consists of *Etheostoma stigmaeum* from the Cahaba River and Gravel Creek, which are tributaries to the Alabama River that drains the coastal plain of Alabama. These samples are also

recovered as sister and have a well-supported relationship. Mean intraclade divergence is 0.0085.

6. Mississippi Coastal Plain Clade – The Alabama Coastal Plain clade is sister to the Mississippi Coastal Plain Clade, and this relationship is fairly well supported. Internally, the Mississippi coastal plain clade is comprised of the Pascagoula, Pearl, and Amite. The clade is well-supported, but the Pearl River is paraphyletic as the Topisaw Creek samples do not form a monophyletic group with the Strong River and Turkey Creek samples. Samples from both the East Fork of the Amite River and Bowie Creek in the Pascagoula basin are recovered as monophyletic. Mean intraclade divergence is 0.0095.

Interclade divergence estimates are given in Table 3.3. The greatest divergence occurs between the undescribed species and the six clades.

ND5 Gene

Seventy-one individuals were sequenced for phylogenetic analysis of the ND5 gene. The aligned ND5 consisted of 751 bases, 576 of which were non-informative, leaving 175 PI characters. The heuristic search recovered 200 equally MPTs with a L of 362, a CI of 0.58, and an RI of 0.88. Thirty-eight nodes were collapsed on the strict-consensus tree (Fig. 3.7). The topology of the strict-consensus tree recovered from analysis of the mitochondrial ND5 gene varies from the topology of the strict-consensus tree recovered from the analysis of the mitochondrial cyt *b* gene.

Unlike the cyt *b* topology, *Etheostoma akatulo* is recovered as sister to all remaining *Doration*. This finding supports the hypothesis of Layman (1994) stating that *Etheostoma akatulo* was the basal member of *Doration*. *Etheostoma meadiae* is recovered as sister to the bluegrass, longhunt and clown darters and *Etheostoma jessiae*. Also unlike the cyt *b* topology, the bluegrass, longhunt, and clown darters are each recovered as monophyletic. These clades are recovered as sister to the Western Mississippi, Coosa, Alabama Coastal Plain, Eastern Mississippi, Mississippi Coastal Plain, and Tenn-Tom clades. Internally, the clades are well-supported and some

additional differences between the cyt *b* and ND5 topologies exist. On the ND5 topology, the Pearl River samples of the Mississippi Coastal Plain clade are fully resolved. The Tenn-Tom clade is recovered as paraphyletic as one of the Noxubee River samples groups with the Mississippi Coastal Plain clade. Further, within the Tenn-Tom clade, the Black Warrior River drainage is no longer monophyletic, as a sample from its tributary, Minter Creek, is recovered as sister to the Sucarnoochee River sample. Intra- and interclade divergence estimates are comparable to those obtained from the cyt *b* gene (Table 3.4).

Concatenated Cyt b and ND5 Datasets

Sequences for 79 individuals, 67 of which contained sequences for both the cyt *b* and ND5 genes, were included in the concatenated dataset. The aligned concatenated dataset has 1930 characters, 1485 of which are non-informative, leaving 427 PI characters. The heuristic search returned 5000 equally MPTs with a L of 1045, a CI of 0.53, and an RI of 0.85 (Fig. 3.8). Thirty-nine nodes were collapsed on the strict-consensus tree. The strict-consensus tree inferred from the concatenated cyt *b* and ND5 sequences has the same topology as the cyt *b* topology.

Maximum Likelihood Estimation (ML) of Phylogeny

A maximum likelihood (ML) estimation of phylogeny was performed on the concatenated mitochondrial (cyt*b*/ND5) dataset. ML methods are used to choose a tree based on optimized parameters that have the highest probability of providing the given aligned nucleotide dataset (Huelsenbeck and Crandall, 1997). Specific to phylogenetic inference, ML optimizes the likelihood of the topology (T), branch lengths (B), and model (M) used given the dataset, and the likelihood (L) of these variables is proportional to their probability (P) (Zwickl, 2006):

$$L(T, M, B \mid D) \propto P(D \mid T, M, B)$$

The ML analysis was performed using GARLI (Genetic Algorithm for Rapid Phylogenetic Inference) v. 0.951 (Zwickl, 2006). Parallel to the Bayesian analysis, the ML analysis began with

a random tree, and the GTR model with gamma distributed substitution rates was implemented. The analysis was allowed to run until the topology reached stationarity and no additional branch optimizations could occur. The final topology with a log likelihood score of -9290.1391 was reached after 2,208,100 generations, and this score is similar to the score obtained for three separate shorter runs. A non-parametric bootstrap was also performed in GARLI. Bootstrap replicates were set at 100. PAUP (Phylogenetic Analysis Using Parsimony) 4.0b10 (Swofford, 2002) was used to create a majority-rule consensus topology based on the 100 non-parametric bootstrap trees found using GARLI. The ML topology is similar to the topology recovered from analysis of the cyt *b* gene with one major exception – as with the ND5 topology, *Etheostoma akatulo* is recovered as sister to all remaining *Doration* (Fig. 3.9).

Bayesian Estimate of Phylogeny

MrBayes 3.1 (Huelsenbeck and Ronquist, 2003; Ronquist and Huelsenbeck, 2005) was used to perform a Bayesian analysis of the concatenated mitochondrial (cyt *b*/ND5) datasets to assess the posterior probability of the clades in the strict-consensus tree given 79 aligned DNA sequences provided. Specific to phylogenetics, Huelsenbeck and Ronquist (2003) apply Bayes theorem as follows:

$$f(\tau, \nu, \theta \mid X) = f(\tau, \nu, \theta) f(X \mid \tau, \nu, \theta) / f(X)$$

X represents the sequences, τ represents the tree topology, ν represents the branch lengths, and θ represents the substitution model. To the left of the equal sign is the posterior probability and to the right are the priors and likelihood function divided by the total probability of all data.

The sequences for each gene were partitioned, and the default flat priors were implemented under the General Time Reversal (GTR) evolutionary model due to its relaxed parameters. The GTR model has a substitution type for each pair of nucleotides (AC, AG, AT, CG, CT, CG), and substitution rates were set as gamma distributed. Two simultaneous independent runs of the data

were utilized. To increase the computing efficiency of the analyses, the Metropolis Coupling settings, which enhance the Markov chain Monte Carlo (MCMC) sampling, were altered to accommodate the concatenated dataset. The independent analyses began with separate random trees chosen by the program. Both runs utilized six chains – five heated and one cool – that were set at a temperature of 0.1. Chains were sampled every 1000th generation with the swap frequency set at two which allowed two randomly chosen chains – one heated and one cool – to attempt to swap their states. Two swaps were attempted per chain swap. The analysis was ended when the standard deviation of split frequencies for the two independent runs fell below the stop value of 0.01.

The standard deviations of split frequencies fell to 0.009691 after 1.5 million generations and the analyses were ended. The first 375,000 generations were discarded as burn-in. As every 1000th generation was sampled, there were 1500 samples included in the posterior probability with the first 375 samples discarded as burn-in. The posterior probabilities are mapped onto the ML topology (Fig. 3.9).

S7 Gene

Thirty-four individuals were sequenced for phylogenetic analysis of the S7 gene. The aligned S7 dataset consisted of 630 bases, 584 of which were constant, leaving 46 PI characters. The heuristic search returned 322 equally MPTs with a L of 86, a CI of 0.59 and an RI of 0.76. Seventeen nodes were collapsed on the strict-consensus tree (Fig. 3.10).

Analysis of the S7 gene yielded little variability. *Etheostoma akatulo* was recovered as sister to all *Etheostoma stigmaeum* analyzed. The majority of the S7 topology is collapsed into a polytomy with minor structure. The longhunt and highland darters and the Alabama Coastal Plain clade are recovered as monophyletic. Similar to the cyt *b* topology, the Mississippi Coastal Plain clade is recovered as paraphyletic with the East Fork of the Amite River occurring twice on the S7 topology. Due to a lack of structure, divergence estimates were not calculated for the S7 gene

Table 3.3

Interclade Divergence Estimates Based on the Cyt b *Gene*

	E. akatulo	***E. jessiae***	***E. meadiae***	**clown darter**	**bluegrass darter**	**longhunt darter**	**MS-CP**	**AL-CP**	**Coosa**	**WMR**	**EMR**	**Tenn-Tom**
E. akatulo												
E. jessiae	0.095											
E. meadiae	0.1	100										
clown darter	0.1	0.058	0.097									
bluegrass darter	0.1	0.041	0.096	0.02								
longhunt darter	0.095	0.032	0.097	0.02	0.042							
MS-CP	0.1	0.056	0.095	0.058	0.064	0.057						
AL-CP	0.1	0.071	0.098	0.069	0.071	0.068	0.033					
Coosa	0.096	0.051	0.095	0.058	0.062	0.058	0.031	0.044				
WMR	0.1	0.055	0.09	0.055	0.061	0.048	0.024	0.039	0.026			
EMR	0.1	0.057	0.095	0.057	0.061	0.055	0.041	0.055	0.042	0.036		
Tenn-Tom	0.098	0.055	0.089	0.057	0.057	0.06	0.034	0.045	0.036	0.029	0.043	

Table 3.4

Interclade Divergence Estimates Based on the ND5 Gene

	E. akatulo	***E. jessiae***	***E. meadiae***	**clown darter**	**bluegrass darter**	**longhunt darter**	**MS-CP**	**AL-CP**	**Coosa**	**WMR**	**EMR**	**Tenn-Tom**
E. akatulo												
E. jessiae	0.099											
E. meadiae	0.09	0.069										
clown darter	0.096	0.027	0.067									
bluegrass darter	0.1	0.049	0.078	0.036								
longhunt darter	0.1	0.029	0.072	0.013	0.041							
MS-CP	0.095	0.056	0.062	0.047	0.047	0.052						
AL-CP	0.091	0.056	0.059	0.049	0.055	0.054	0.025					
Coosa	0.1	0.044	0.068	0.041	0.054	0.048	0.038	0.038				
WMR	0.087	0.052	0.052	0.04	0.049	0.049	0.019	0.02	0.034			
EMR	0.1	0.053	0.063	0.039	0.055	0.049	0.039	0.039	0.042	0.035		
Tenn-Tom	0.098	0.046	0.058	0.04	0.043	0.045	0.025	0.029	0.029	0.033	0.055	

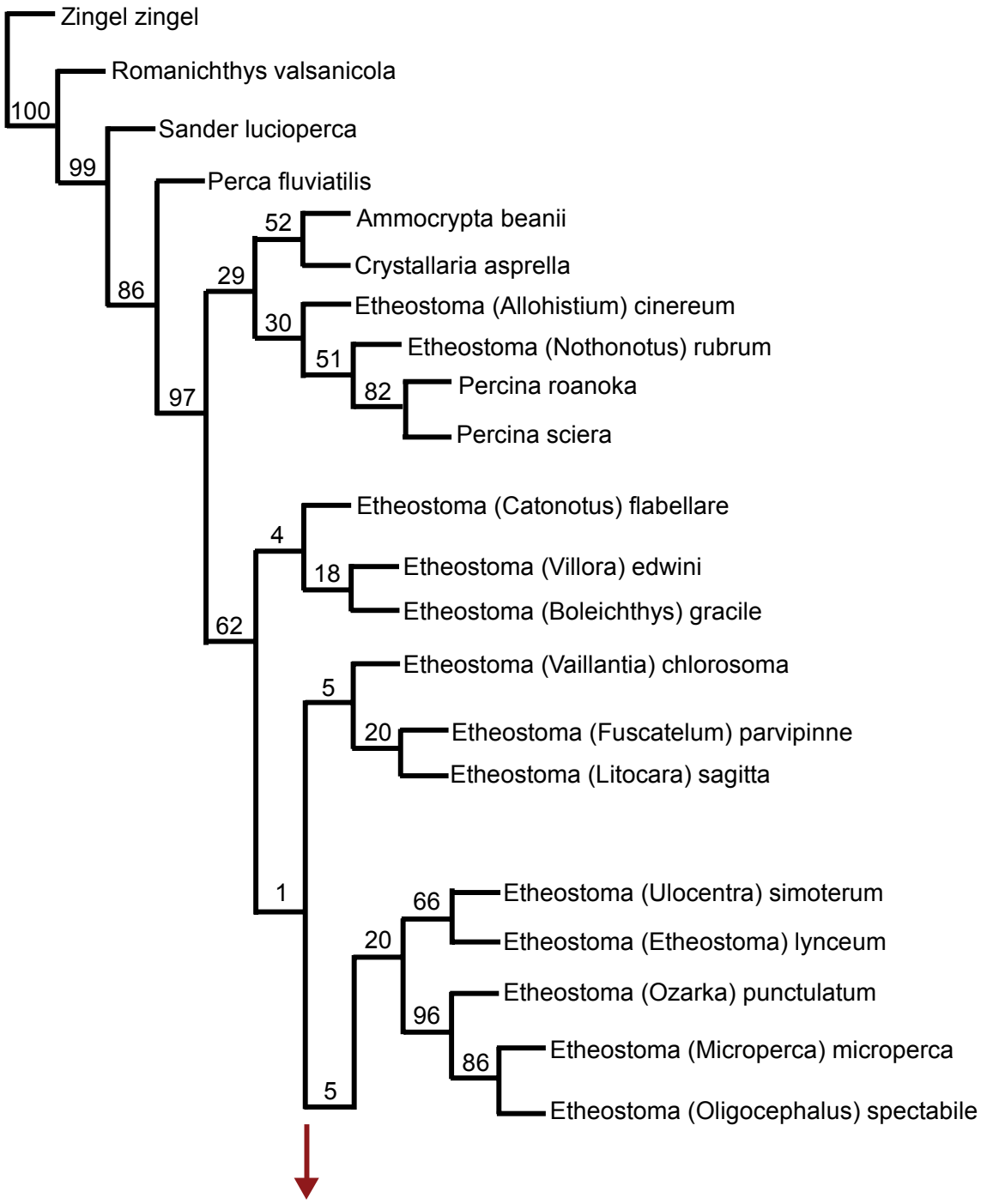

Fig. 3.6. Cytochrome *b* strict-consensus topology. Bootstrap support values are given above branches. L = 2898, CI = 0.27, and RI = 0.61. Individuals sequenced per drainage are identified by the number following the name. Figure is continued on the next page.

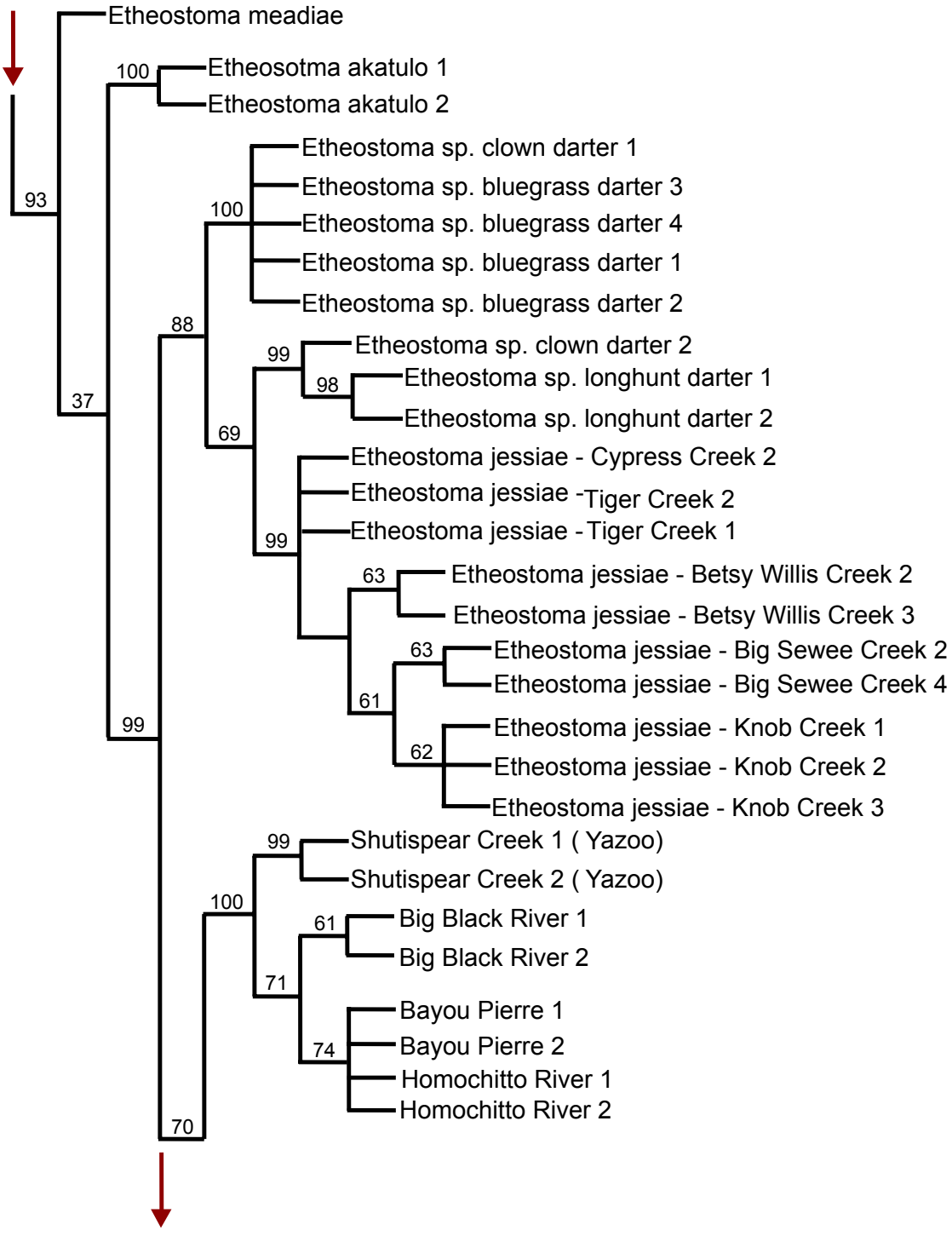

Fig. 3.6. (Continued). Cytochrome *b* strict-consensus topology. Figure is continued on next page.

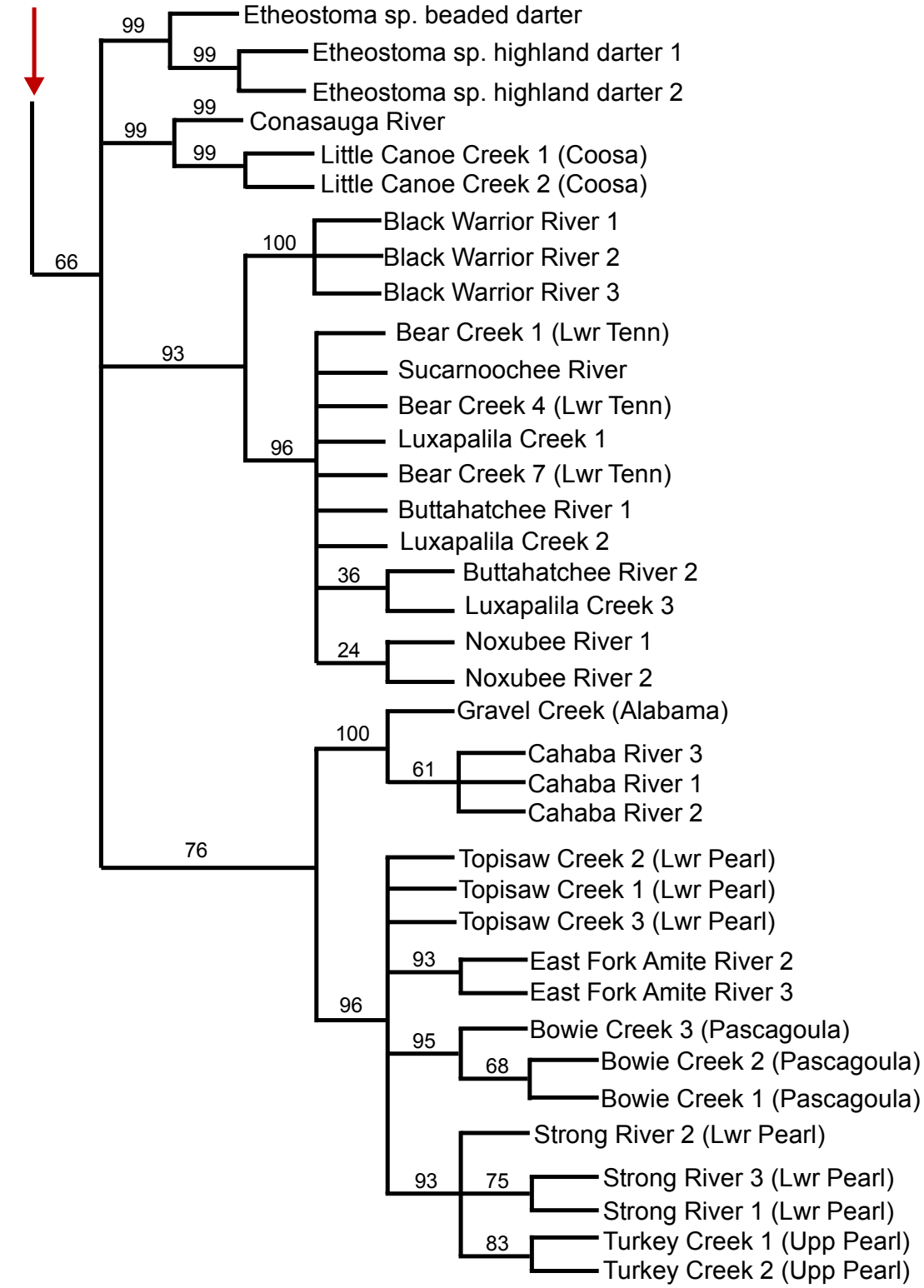

Fig. 3.6. (Continued). Cytochrome *b* strict-consensus topology.

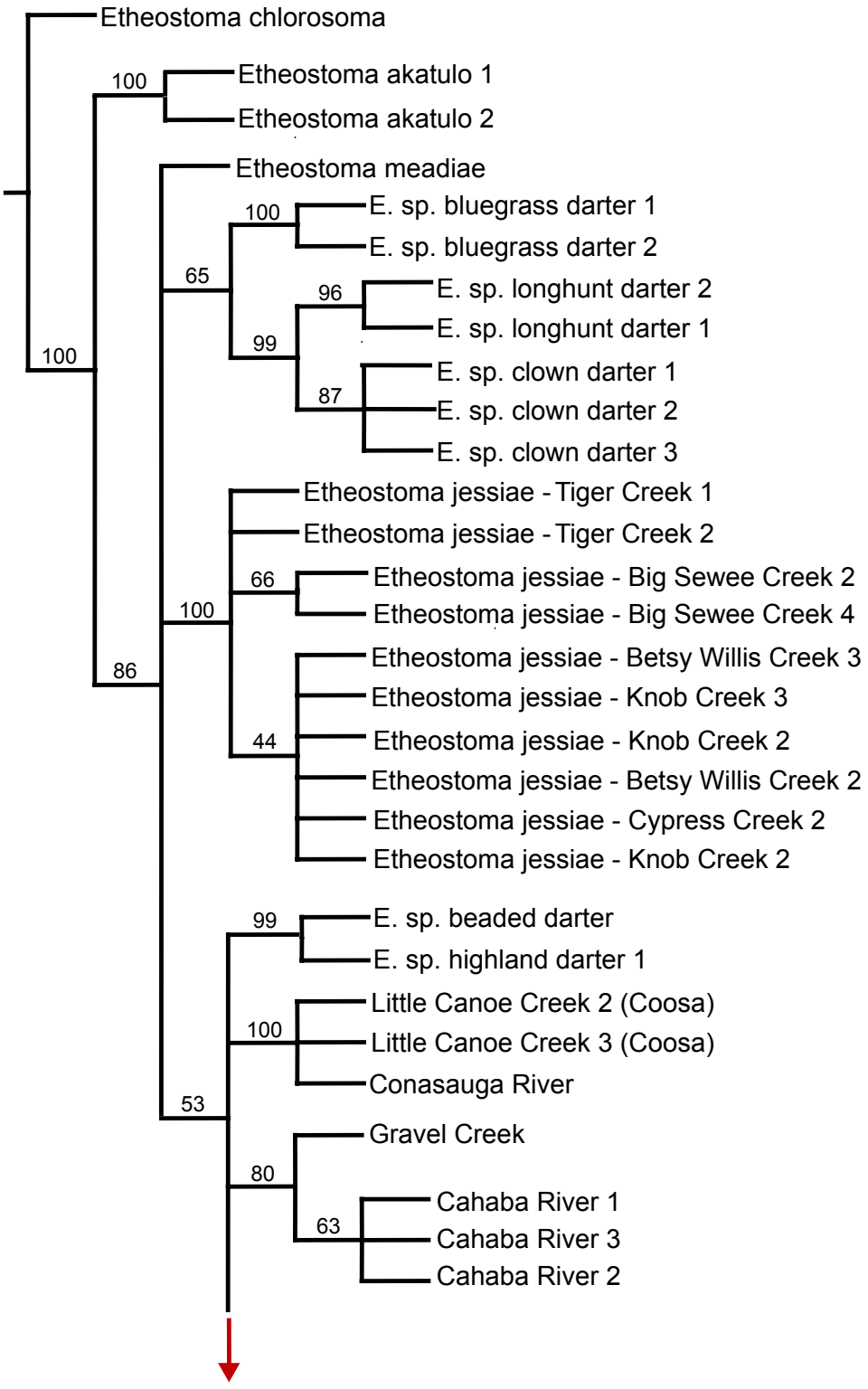

Figure 3.7. ND5 Strict-consensus topology. Bootstrap support values given above branches. L = 362, CI = 0.58, RI = 0.88. Individuals sequenced per drainage are identified by the number following the name. Figure is continued on the next page.

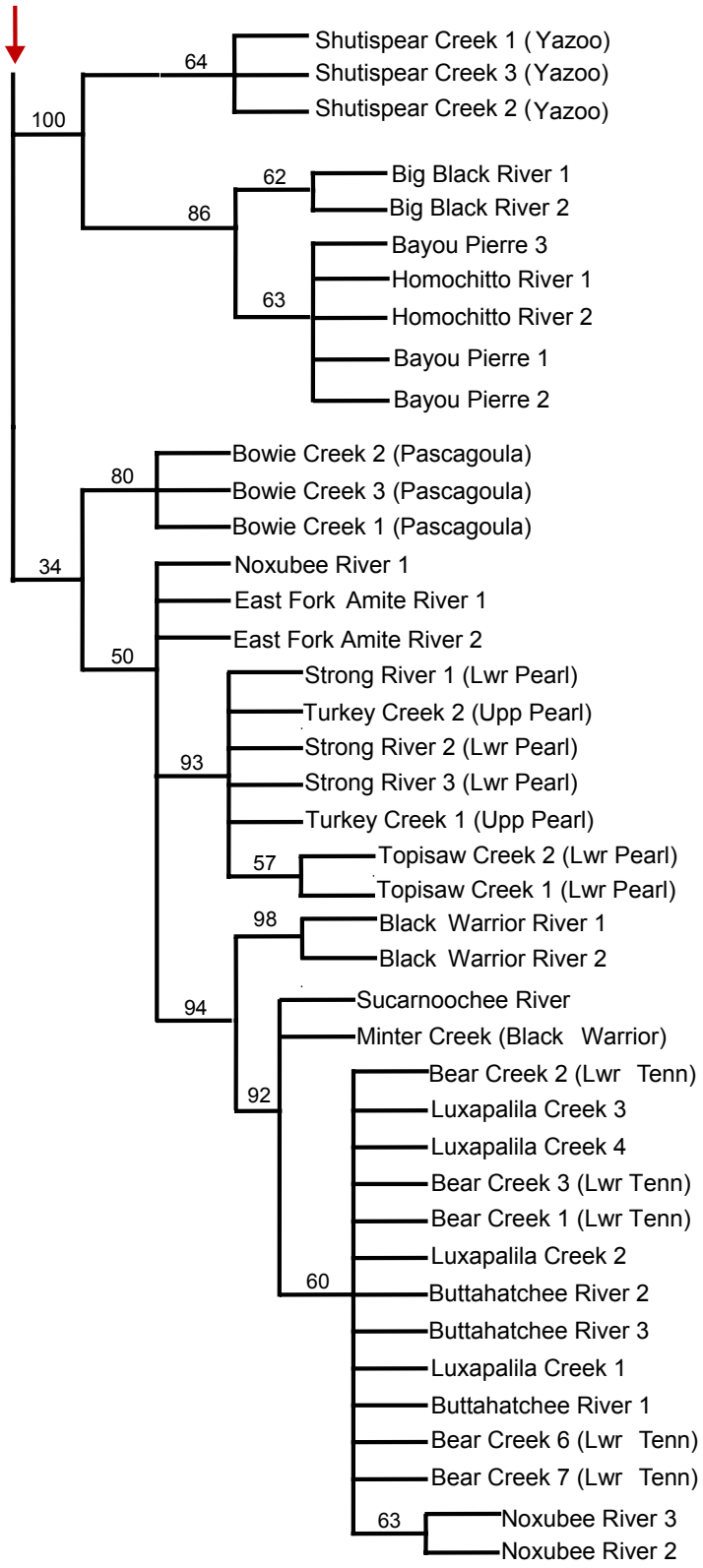

Fig. 3.7. (Continued). ND5 strict-consensus topology.

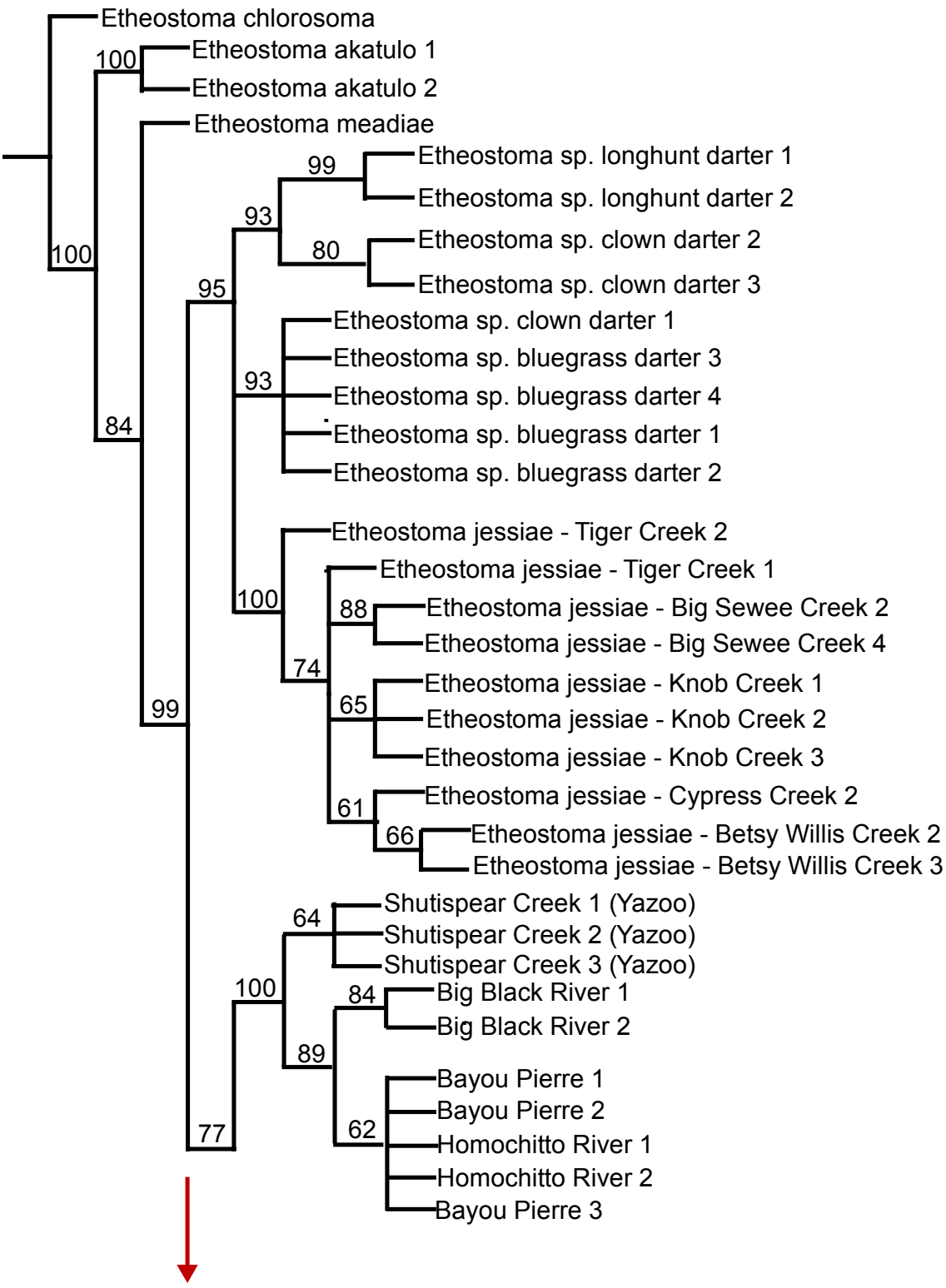

Fig. 3.8. Concatenated cytochrome *b* and ND5 strict-consensus topology. Bootstrap support values given above branches. L = 1045, CI = 0.53, RI = 0.85. Individuals sequenced per drainage are identified by the number following the name. Figure is continued on the next page.

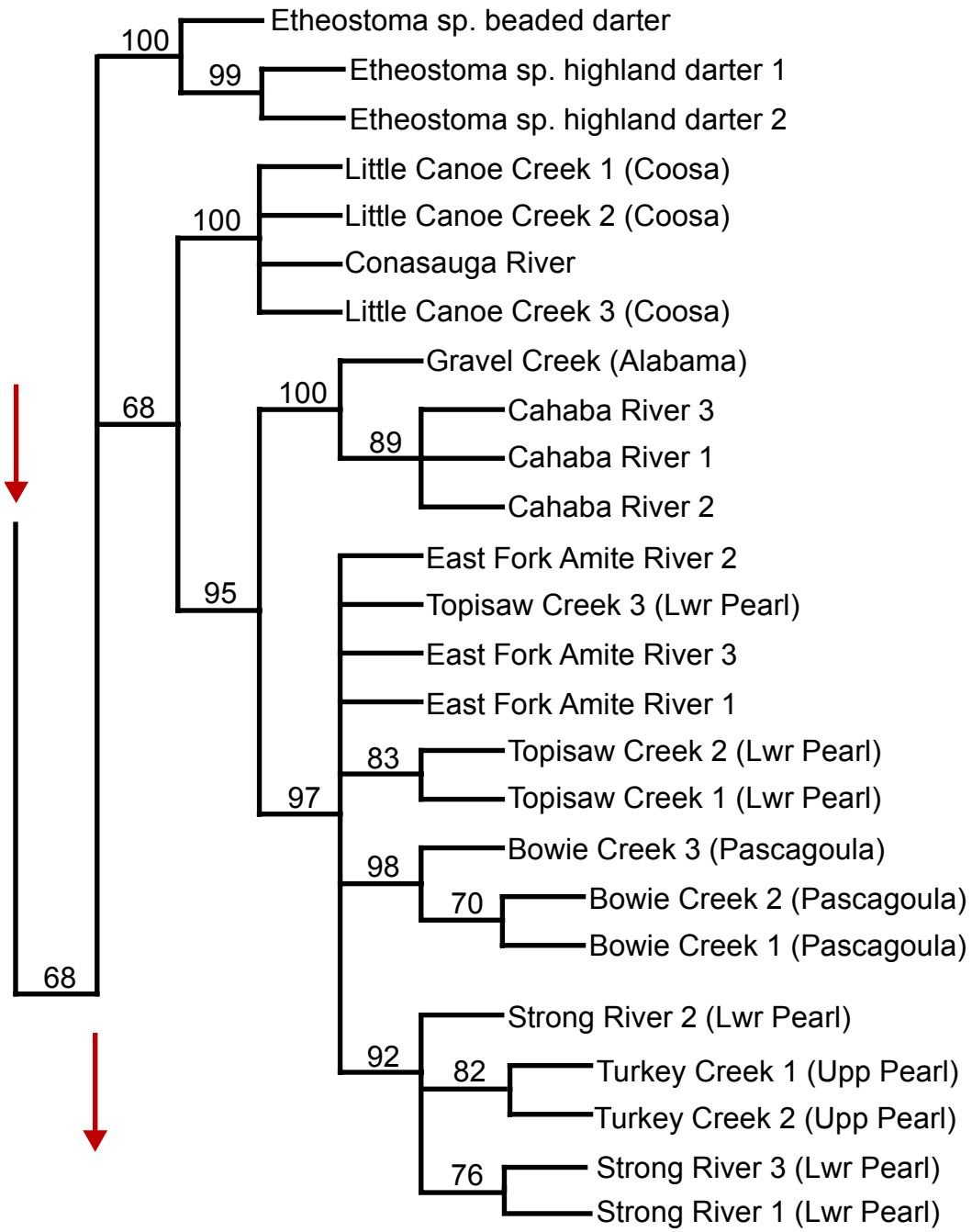

Fig. 3.8. (Continued). Concatenated cytochrome *b* and ND5 strict-consensus topology. Figure is continued on the next page.

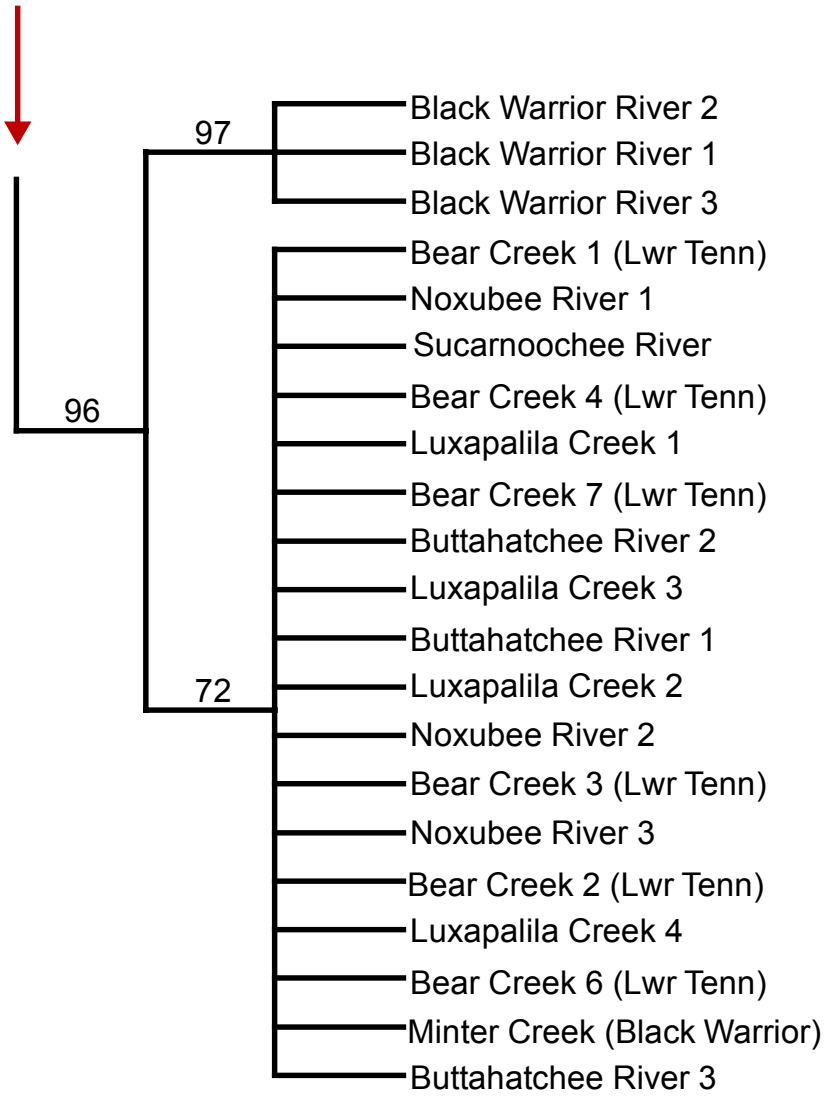

Fig. 3.8. (Continued). Concatenated cytochrome *b* and ND5 strict-consensus topology.

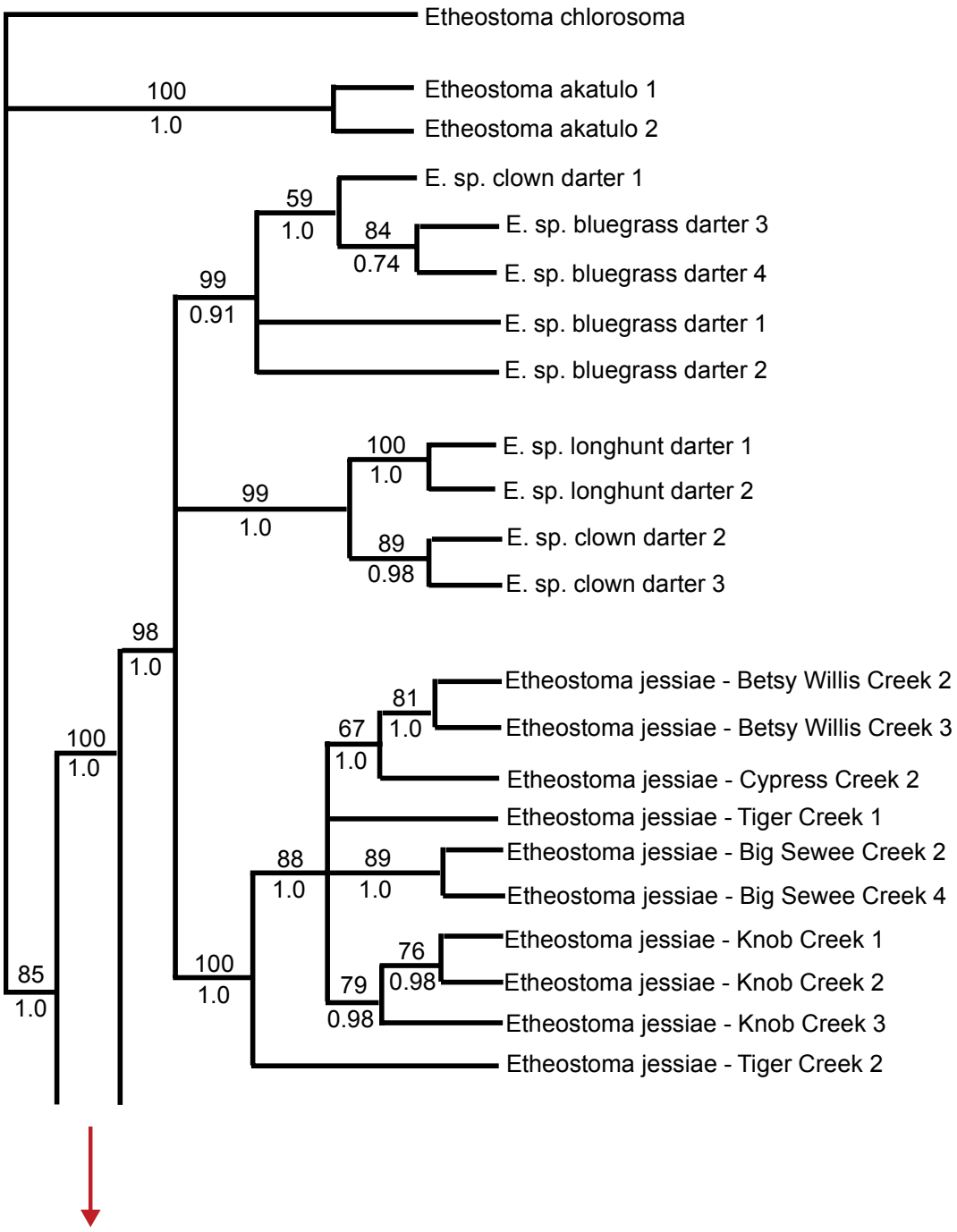

Figure 3.9. Maximum likelihood topology inferred from the concatenated cyt b/ND5 datasets. Bootstrap support values given above the branches. Bayesian posterior probabilities given below branches. Figure is continued on the next page.

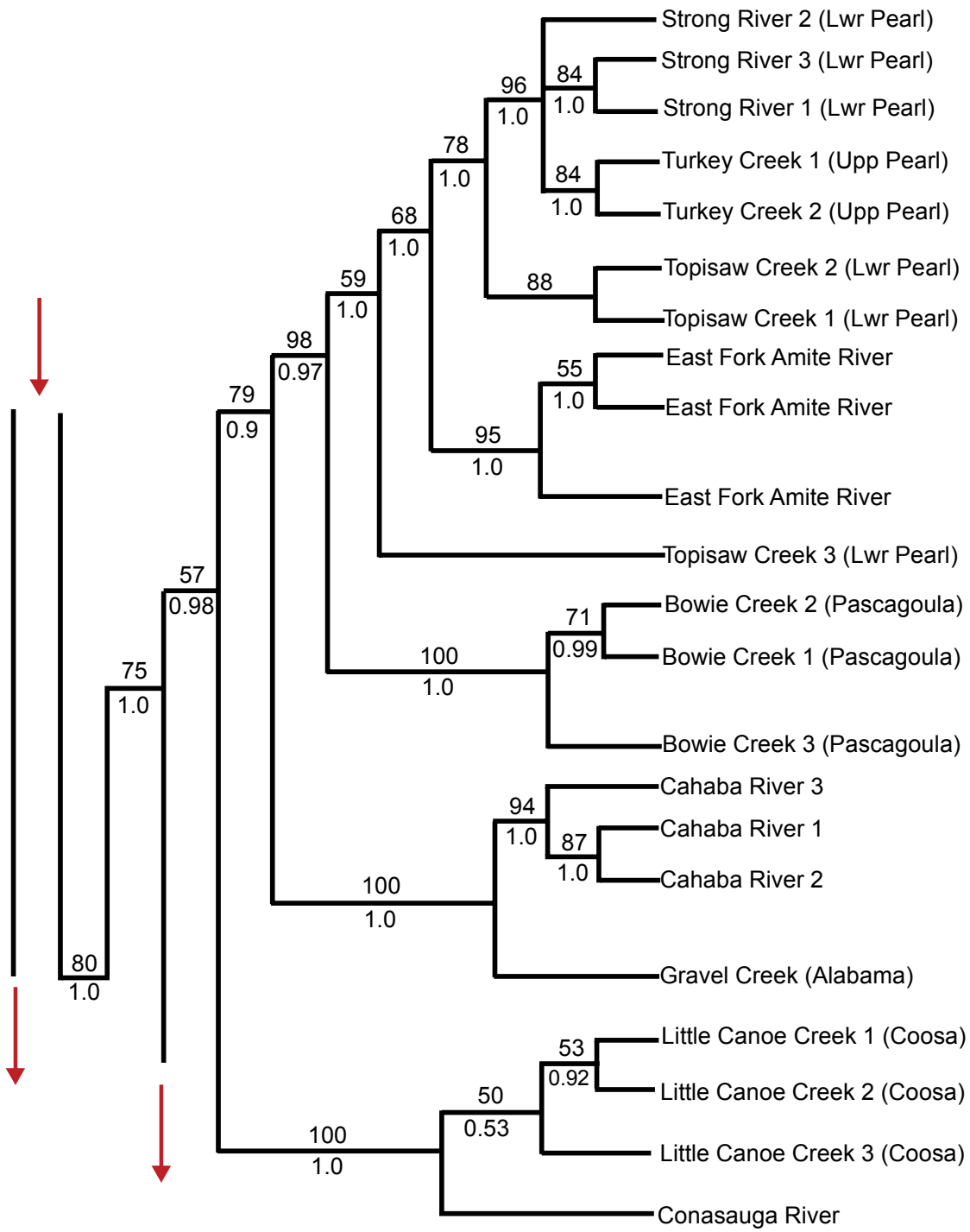

Figure 3.9. (Continued). Maximum likelihood topology inferred from the concatenated cyt b/ND5 datasets. Figure is continued on the next page.

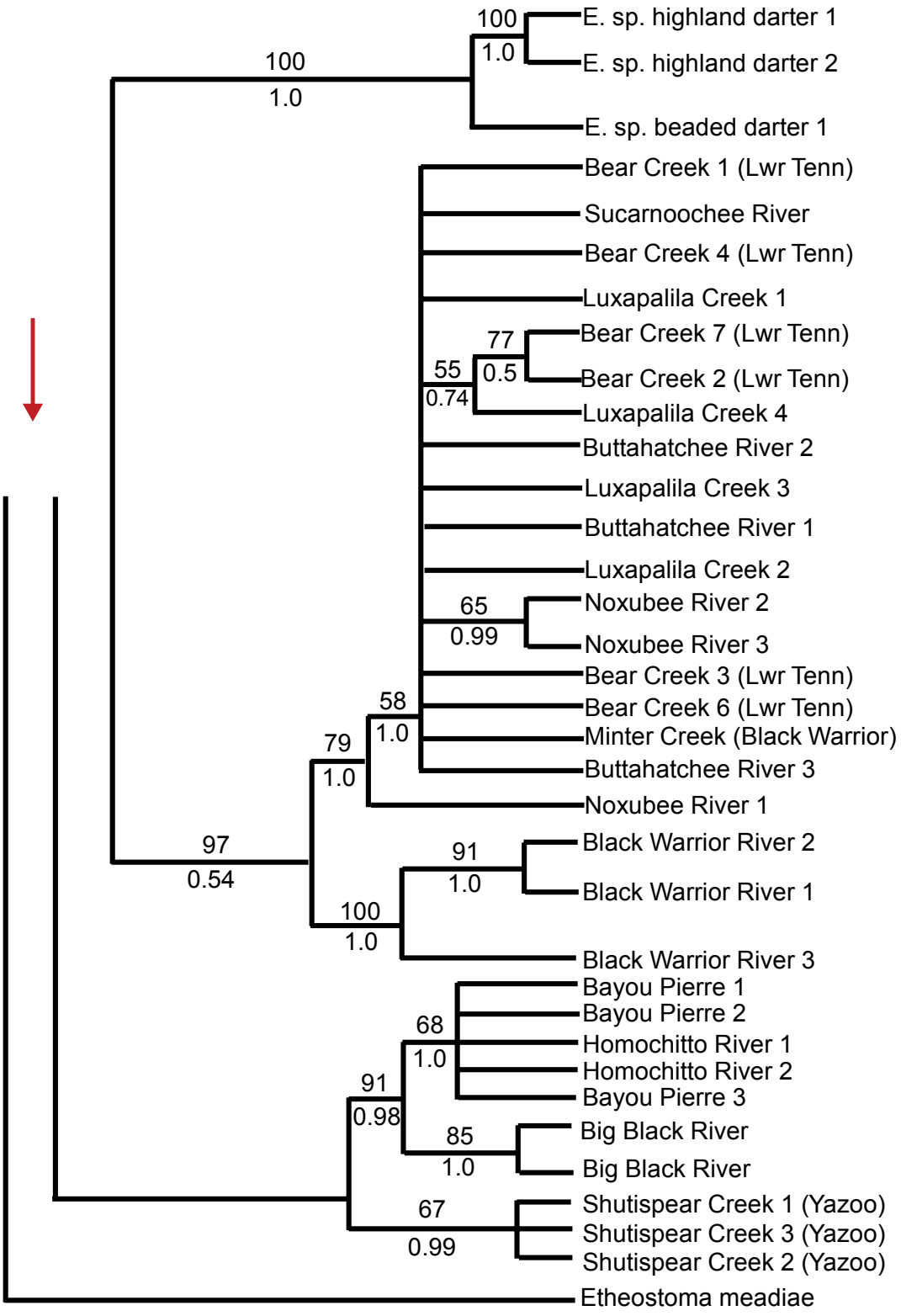

Figure 3.9. (Continued). Maximum likelihood topology inferred from the concatenated cyt b/ND5 datasets.

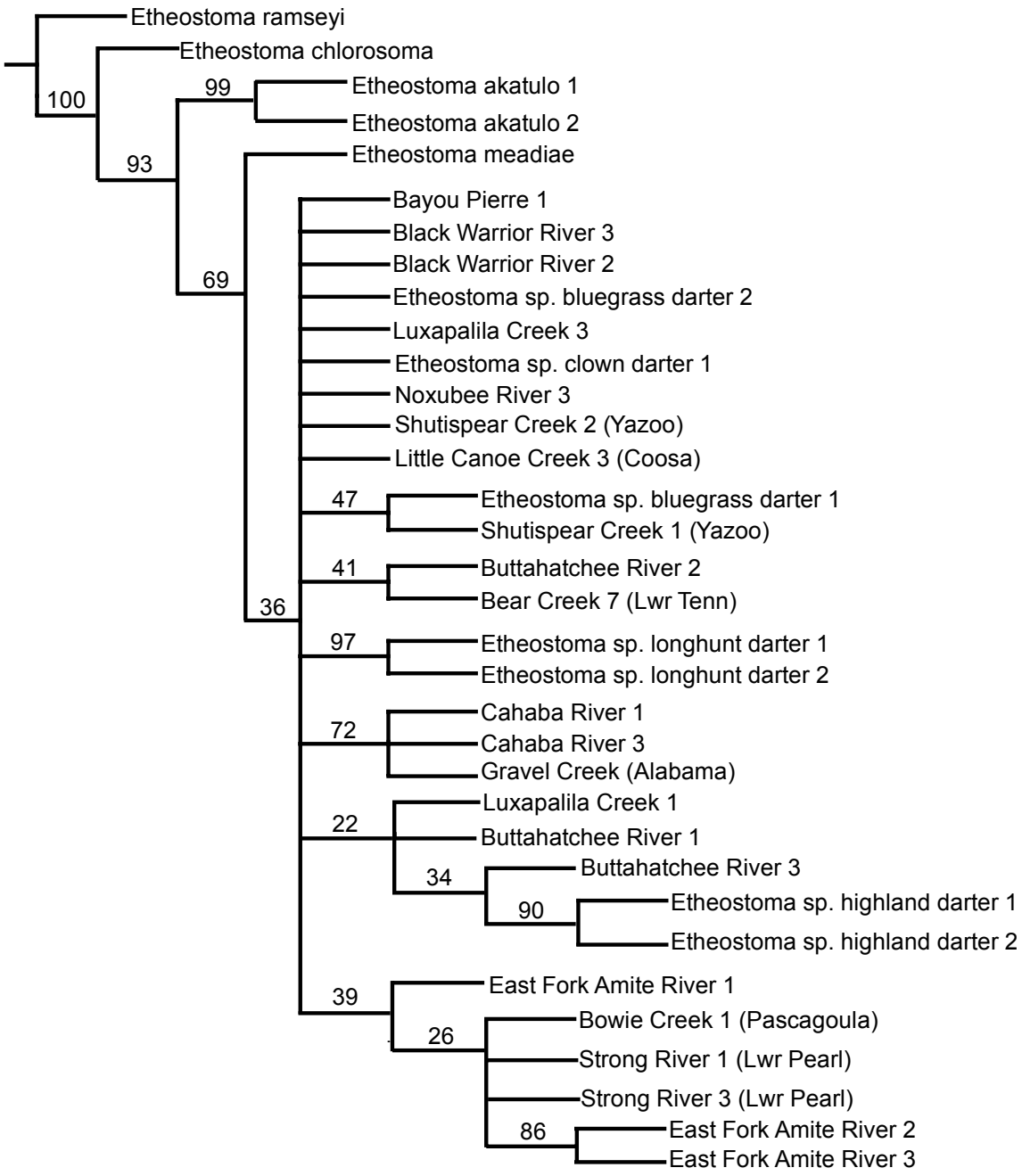

Fig. 3.10. S7 strict-consensus topology. L = 86, CI = 0.59, RI = 0.76.

Discussion

The phylogenies inferred from the mitochondrial cyt *b* and ND5 genes support the monophyly of *Doration*. The cyt *b* topology recovers *Etheostoma meadiae* as sister to all remaining *Doration*, but support for this relationship is low. On the ND5, ML, and S7 topologies *Etheostoma akatulo* is recovered as sister to all remaining members of *Doration* as hypothesized by Layman (1994), and this relationship is well-supported. *Etheostoma meadiae*, the bluegrass, clown, and longhunt darters, and *Etheostoma jessiae* are recovered as basal to all remaining *Doration*. Relationships among the bluegrass, clown, and longhunt darters are not resolved on the cyt *b* topology. The clown darter is recovered as paraphyletic on the cyt *b* topolgy, but on the ND5 topology, it is recovered as monophyletic. Based on the allozyme and morphological data of Layman (1994), the possibility exists that the paraphyly of the clown darter on the cyt *b* topology is the result of a sequencing error. Alternatively, the cyt *b* toplogy may be correct and reflect differing rates of evolution for the cyt *b* and ND5 genes, a historical introgression event between the clown and bluegrass darters, gene duplication, or lineage sorting that mimics an introgression (Doyle, 1992). Unfortunately, the nuclear S7 topology provides no resolution to the conflicting mitochondrial gene trees.

Etheostoma jessiae is consistently recovered as monophyletic, and intraclade divergence estimates suggest that little divergence has occurred among its populations. Also consistently recovered is the well-supported sister relationship of the highland and beaded darters. These relationships suggest that the initial divergence within the subgenus occurred primarily in drainages that flank the Nashville Dome, and resulted in the presence of endemics around the Nashville Dome. The high level of endemicity around the Nashville Dome has previously been recognized (e.g., Powers and Mayden, 2007) and suggests that the ancestral stocks of fishes may have evolved in response to the breaching of the Nashville Dome. Potentially, the breaching led to small vicariant events in the drainages around the dome that resulted in the evolution of the bluegrass darter in the Barren and Green Rivers and the evolution of the longhunt darter in the

Red and Rockcastle Rivers on the northern flanks of the Nashville Dome. East of the Nashville Dome, *Etheostoma meadiae* is found in the Clinch and Powell Rivers of the upper Tennessee River basin, while to the south of the Nashville Dome, *Etheostoma jessiae* is found in the lower Tennessee River basin. Finally, the clown darter is endemic to the Duck/Buffalo system to the west of the dome.

Etheostoma stigmaeum from the Mississippi River drainages (Yazoo, Big Black, Bayou Pierre, and Homochitto) are consistently recovered as a clade. Within this clade, Bayou Pierre and the Homochitto River are recovered as a polytomy, indicating that they share a similar history. Based on the proximity of the Bayou Pierre and Homochitto drainages, it is possible that stream piracy between their tributaries has occurred.

The drainages of the Mississippi coastal plain (Amite, Pearl, and Pascagoula) are also consistently recovered as a clade. Within this clade, the Pascagoula is recovered as monophyletic on all topologies, but the Amite and Pearl are recovered as paraphyltic. This finding indicates that the drainage history of the Pascagoula is independent of the Pearl and the Amite drainages. Similar to the Bayou Pierre and Homochitto Rivers, the Pearl and Amite drainages are in proximity to one another, and stream piracy events between their tributaries may have occurred.

The Tenn-Tom clade is composed of a polytomy inclusive of the Bear Creek drainage of the lower Tennessee and the major tributaries to the Tombigbee River, exclusive of the Black Warrior River. This polytomy may be the result of a retained ancestral polymorphism, whereby the ancestor had multiple character states, but the samples selected retain only a few of these character states, which conflict internally. Recently, Keck and Near (2010) recognized the occurrence of mitochondrial replacement in the *Etheostoma* subgenus *Nothonotus* which occurred as a result of the introgression of an unsorted ancestral polymorphism. Based on the findings of Keck and Near (2010), it is possible that the lack of variability among the Tenn-Tom clade may be the result of gene flow between the drainages of the Tombigbee and Bear Creek. Finally, the polytomy may be the result of convergent evolution whereby a specific character became fixed

because it coded for a specific function advantageous to the *Etheostoma stigmaeum* in the lower Tennessee and Tombigbee Rivers. Further, this result reinforces the meristic and allozyme data of Howell (1968), Wall (1968) and Layman (1994) which also showed that the *Etheostoma stigmaeum* in Bear Creek were closely allied to the *Etheostoma stigmaeum* in the Tombigbee River. Wall (1968) suggested that a stream capture had occurred when tributaries to the Buttahatchee River headcut into the tributaries of Bear Creek, but this finding does not necessarily indicate a direct connection between the Tennessee and Mobile basins via Bear Creek. Shaw (1918) noted that, although the Bear Creek valley is wide, it is not wide enough to facilitate a river as large as the Tennessee. Bear Creek makes a northeastern swing through Mississippi before connecting to the Tennessee River. This course is symmetrical to that of the Tennessee River through northeastern Mississippi and suggests that the event that caused the Tennessee to turn northward may have also affected the course of Bear Creek. The possibility also exists that Bear Creek flowed directly into the Tombigbee River prior to this event, but this possibility has not been geologically investigated.

The Coosa and Alabama coastal plain drainages are consistently recovered as sister, but this relationship is not well-supported. It would be expected that support for a relationship between the two would be high as the drainages in these clades are currently connected.

When assessed under the Phylogenetic Species Concept (PSC) *sensu stricto* Nixon and Wheeler (1990), the evidence from the molecular analyses employed support the existence of at least nine species within *Doration* as proposed by Layman (1994). Both the described species (*Etheostoma stigmaeum*, *Etheostoma jessiae*, *Etheostoma meadiae*, and *Etheostoma akatulo*) and the undescribed beaded, bluegrass, clown, highland, and longhunt darters were recovered as monophyletic terminal lineages with no *a priori* expectations of monophyly, demonstrating that the recovered terminal lineages have a “unique combination of character states” (Nixon and Wheeler, 1990, p. 218) for the both the morphological (Layman 1994) and DNA characters. Further, *Etheostoma jessiae*, *Etheostoma meadiae*, *Etheostoma akatulo*, and the five undescribed

species are endemic, leading to the expectation that no gene flow exists between their respective populations. One exception to this argument exists. The clown darter is recovered as paraphyletic on both the cyt *b* and ML topologies but is resolved as monophyletic on the ND5 topology. As mentioned above, it is possible that the paraphyly of the clown darter is the result of a sequencing error because when considered with the unique morphological characteristics described by Layman (1995), a strong case exists for ascribing species status to the clown darter. Further, the species status of *Etheostoma meadiae* has been questioned with some arguing that *Etheostoma meadiae* is the product of intergradation between *Etheostoma stigmaeum* and *Etheostoma jessiae* (e.g. Burkhead and Jenkins, 1994), but neither the mitochondrial nor nuclear data provide support for hybridization or introgression. Under the PSC, *Etheostoma meadiae* is a valid species. It is consistently recovered as a monophyletic terminal lineage, is endemic, and based on the analyses of Layman (1994), has unique morphological attributes.

These findings also lend support to the Central Highland Vicariance Hypothesis (CHVH) of Wiley and Mayden (1985) and Mayden (1988). The CHVH basically states that, prior to the Pleistocene, a widespread highland fauna existed that was cradled between Ozark-Ouachita and Appalachian Mountains and during the Pleistocene, this fauna was splintered due to glacial advances and retreats. This finding is in contrast to Starnes and Etnier (1986) who proposed that *Etheostoma stigmaeum* originated in habitats of the lower Mississippi River or habitats in the western drainages of the Gulf Coast, and subsequently dispersed north via the Mississippi River.

The beaded and the highland darters from the Ouachitas and Ozarks respectively are also differentiated, though whether this is the result of a vicariant event as predicted by the CHVH or by dispersal is unclear. This clade is recovered as sister to the Tenn-Tom and coastal plain clades. It would be expected that the highland and beaded darters would be closely related to the Mississippi River clade as found in species of the *Etheostoma* subgenus *Nothonotus*, where *Etheostoma moorei* from the Ozarks is sister to *Etheostoma rubrum* in the Bayou Pierre system (Wood, 1996).

With respect to the drainage hypotheses under investigation, Hayes and Campbell (1894) hypothesized that the ancestral Tennessee River flowed towards the Mississippi Embayment in a course that approximated the Big Black River. Overall, the evidence from the phylogenetic trees inferred from analysis of the mitochondrial cyt *b* and ND5 genes, their concatenated sequences, and the nuclear S7 gene neither support nor refute this hypothesis. Furthermore, the inferred trees neither support nor refute the hypothesis of Galloway (2005) who hypothesized that an extra-basinal Tennessee River flowed across Mississippi with an outlet to the Gulf of Mexico via the lower Pearl River; however, based on the volume of material breached from the Nashville Dome, it would be expected that the extra-basinal Tennessee River system would be of a size akin to the modern Tennessee or the modern Mississippi and carry a high bedload which would act as a barrier to dispersal rather than facilitate the movement of organisms that are small and not vagile. It is possible that, historically, drainages such as the Black Warrior were tributaries to the extra-basinal system, which may explain why the Black Warrior itself is recovered as a monophyletic clade that is sister to the rest of the Tenn-Tom clade. Further, if this system prevented dispersal, it would be expected that the fishes in the drainages that were tributaries to the system would have remained in their respective basins, which would explain why the Mississippi, Tombigbee, and coastal plain drainages are recovered as individual clades with strong internal support but poor interclade support. Based on this scenario, it is difficult to discern how *Etheostoma stigmaeum* reached the coastal plain drainages, but there are at least four explanations. The fishes may have entered drainages of the Mississippi coastal plain via the ancestral Mississippi. *Etheostoma caeruleum* provides a model for this scenario as it is found extensively throughout the Tennessee River basin and in the Homochitto River system that drains across the coastal plain of Mississippi, but is absent from intermediate drainages such as the Pearl (Etnier and Starnes, 1993; Ross, 2001). Alternatively, as the amount of eroded material being transported by the extra-basinal system decreased, it would be expected that the volume of water and bedload transported by the system would have also decreased, which may have provided an opportunity for dispersal

from some of the tributaries to the extra-basinal system into the drainages of the coastal plain. For example, once high volume flow waned, *Etheostoma stigmaeum* from the upper Pearl would be able to disperse onto the coastal plain and into the lower Pearl and adjacent drainages. This hypothesis would explain the sister relationship observed between the upper Pearl and lower Pearl and the lack of resolution observed between the Pascagoula, Pearl, and Amite. *Etheostoma stigmaeum* may have reached the coastal plain via the Coosa River basin. The modern courses of the rivers in the Coosa basin are reflected in the results of the phylogenetic analysis and the Coosa clade is recovered as sister to the remaining coastal plain drainages, albeit with low bootstrap support. Finally, Isphording (1983) hypothesized that once the ancestral Tennessee reached Guntersville, Alabama, it continued on a southwestward course that crossed Alabama onto the coastal plain of Mississippi. This hypothesis would explain the sister relationship between the Alabama coastal plain clade and the Mississippi coastal plain clade recovered on the ND5 tree.

The hypothesis of Shaw (1918) that the headwaters of the Big Black River were captured from the Pearl River during the Pliocene is not supported by the topologies of the mitochondrial gene based trees. Based on transversion rates in cyt *b*, Song (1994) estimated that diversification within *Etheostoma* occurred during the Miocene. The timing of this diversification predates the Pliocene capture envisioned by Shaw (1918), and it would be expected that, due to a lack of diversification time, the Big Black and Pearl Rivers would be recovered in a clade together, but the two are recovered in separate clades on all mitochondrial gene based trees. This lack of diversification time may also explain the lack of well-supported structure with the Coastal Plain clade. It is likely that *Etheostoma stigmaeum* reached the drainages of the coastal plain during the Plio-Pleistocene when sea level was lower and the coastal plain and shelf were exposed, an event which also post-dates the divergence estimate of Song (1994).

Several difficulties were incurred with using the phylogenetic systematics of *Etheostoma stigmaeum* to test hypotheses regarding the evolution of the Tennessee River. First, the

mitochondrial cyt *b* and ND5 genes provided more variability than the nuclear S7 gene. A similar result was obtained by Keck and Near (2008) in their analyses of the *Nothonotus* group of darters. Nuclear genes are biparentally inherited, involve recombining loci, may be subjected to concerted evolution, and tend to evolve in response to specific environment stressors (Doyle and Davis 1998; Rand 2001) whereas mitochondrial genes are typically passed from one generation to the next through only the maternal lineage (but see Walker et al., 2006). Belle et al. (2005) found that there was a bias for synonymous transition polymorphisms in animal mitochondrial DNA. Mitochondrial genes, therefore, have an effective population size that roughly equal to the number of females in a population, which is typically one-quarter the effective population size of bi-parentally inherited nuclear genes, allowing for the rapid accumulation of mutations in mitochondrial DNA (Wilson et al., 1985; Birky et al., 1989; Rand, 2001; Funk and Omland, 2003).

Second, interlocus incongruities were found on the topologies inferred from the cyt *b* and ND5 mitochondrial genes. Page et al. (2003) found similar incongruities in their analyses of barcheek darters. These incongruities may occur due to incomplete lineage sorting or a saturation of nucleotide substitutions which appear to be accumulating homoplasies that obscure phylogenetic relationships (Funk and Omland 2003; Mendelson and Simons 2006).

Lastly, *Etheostoma stigmaeum*, with the exception of the lower Bear Creek and Duck River systems, is replaced in the lower Tennessee River by its sister, *Etheostoma jessiae*. This impedes direct comparison of the lower Tennessee to the remaining drainages of Mississippi and Alabama.

Conclusions

Neither the hypotheses of Hayes and Campbell (1894) or Galloway (2005) could be accepted or refuted based on the inferred topologies. Issues incurred with this analysis included a lack of variation in the S7 nuclear gene, interlocus incongruities among mitochondrial genes leading to variable topologies, and difficulties making direct comparisons between the lower Tennessee River and the drainages of Mississippi and Alabama due to the replacement of *Etheostoma*

stigmaeum by *Etheostoma jessiae* in the Tennessee River. Despite these issues, this study represents one of the first comprehensive phylogenetic analyses of aquatic organisms of the Gulf of Mexico coastal plain drainages of Mississippi and Alabama, and further analyses of the coastal plain are needed to assess the relationships of the aquatic organisms of the coastal plain to those of adjacent basins.

In 2009, the Southeastern Fishes Council held a symposium focusing on rivers in the southeastern United States that were given priority status due to special conservation needs. Included in the rivers listed were the Pearl, in both Mississippi and Louisiana, and the Pascagoula in Mississippi. Within the Mobile basin, the Tombigbee, Black Warrior, Conasauga, and Coosa Rivers were listed. Within the Tennessee River basin, portions of the Tennessee River and the Duck River system were listed, and in Kentucky, the Green, Cumberland, Rockcastle, and Barren Rivers were listed (Albanese and Litts, 2009; Bart et al., 2009; Dinkins and Etnier, 2009; Kuhajda, 2009; Slack et al., 2009; Thomas, 2009). *Etheostoma stigmaeum* or *Etheostoma jessiae* from each of these rivers were utilized in this analysis, and the relationships that are inferred from phylogenetic analyses, such as this, can be used by resource managers to make informed decisions regarding the conservation of endemics, the feasibility of translocating species, choosing the appropriate surrogates to infer the life histories of highly imperiled species, and to choose the appropriate brood stock when re-stocking a water body. These issues either are or will be faced by managers charged with the protection of the priority rivers of the southeastern United States.

Studies of widespread organisms often overlook the drainages of the Gulf of Mexico coastal plain (Layman, 1994). Future studies should address this omission, for both the biogeographical and conservation information that such studies can provide. Further tests of the hypotheses regarding the evolution of the Tennessee River should utilize a widespread species that occurs both above and below the fall line. Only by recognizing repeated patterns of differentiation

within species can potential vicariance and dispersal events for the coastal plain be recognized, and the complicated history of the Tennessee River understood.

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CHAPTER IV

GEOLOGICAL AND ICHTHYOLOGICAL INVESTIGATIONS INTO PALAEODRAINAGE HYPOTHESES FOR THE TENNESSEE RIVER: A SYNTHESIS OF THE DATA

Numerous hypotheses have been proposed to explain the course of the Tennessee River, but few of these hypotheses have been rigorously tested. The possibility exists that all of the hypotheses are acceptable as they may reflect events that occurred simultaneously or at different temporal junctures that are superimposed upon one another across the ~350 million year history of the Tennessee River. Many of the proposed drainage hypotheses contain elements similar to those found in Hayes and Campbell (1894). The Appalachian River hypothesis proposed by Hayes and Campbell (1894), which states that during the Tertiary, the upper Tennessee and Coosa River basins were connected by an Appalachian River system, has become ingrained in the biological literature due to the close phylogenetic relationships observed among the aquatic faunas of the upper Tennessee and Coosa River basins. Geological evidence regarding the existence of an Appalachian River is lacking. The lack of geologic evidence does not necessarily negate the hypothesis, but other alternatives should be explored. For example, based on geological evidence, Mills et al. (2005) argue that stream piracy events have occurred between the Ocoee River system of the Tennessee drainage and the Conasauga River system of the Coosa drainage, and this hypothesis could explain not only the close phylogenetic relationships observed between the upper Tennessee and the Coosa, but also the high levels of endemicity observed in headwaters of the Coosa (e.g. Boschung and Mayden, 2004). Hayes and Campbell (1894) further hypothesized that following the piracy of the Appalachian River, the ancestral Tennessee continued across the state of Mississippi before reaching the Mississippi Embayment. Grim (1936) concurred with Hayes and Campbell (1894) arguing that the Wilcox formation in Mississippi contained rocks and minerals that were derived from the Appalachian Mountains. Brown (1967) also hypothesized that the ancestral Tennessee crossed the state of Mississippi and argued that the Pliocene-age Citronelle Formation was a Tennessee River system deposit.

Isphording (1983), based on mineral suites in a salt dome near New Augusta, Mississippi, hypothesized that the ancestral Tennessee continued across Alabama and flowed into the Pascagoula River basin. More recently, Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005) have proposed the existence of an extra-basinal Tennessee River system that existed from the Miocene to the Pleistocene and crossed the state of Mississippi and emptied into the Gulf of Mexico via the lower Pearl River drainage. The extra-basinal Tennessee hypothesis is somewhat a synthesis of the previous hypotheses placing the course of the ancestral Tennessee across Mississippi. Geological evidence in support of an extra-basinal system is strong. The Citronelle Formation, which spans from Texas to Georgia, is recognized as a fluvial deposit, and within Mississippi, the Citronelle contains fossils similar to those found along the Highland Rim of central Tennessee and northern Alabama (Smith and Meylan, 1983). Further, the Citronelle is predominantly chert (Self, 1983; Smith and Meylan, 1983), and the most proximal source of chert is found in the Fort Payne Formation of the Appalachians (Smith and Meylan, 1983). Also, it has been recognized that the lower Pearl River historically had a higher flow regime (Self, 1983; Cotton, 1986). Cotten (1986) mapped the terraces of the lower Pearl, and based on crustal warping rates, estimated that at the Plio-Pleistocene boundary, a major downcutting event occurred which further incised the Pearl River valley. The timing of this downcutting event corresponds with the extra-basinal fluvial system proposed by Combellas-Bigott and Galloway (2002, 2006) and Galloway (2005). To further investigate the existence of an extra-basinal Tennessee River that crossed the state of Mississippi, rare earth element (REE) signatures were compared between cherts collected from the Fort Payne and Citronelle Formations, and the molecular systematics of the *Etheostoma* subgenus *Doration* were used to infer phylogenetic relationships among the basins under investigation.

Results of the REE analyses suggest that Citronelle samples from the Pascagoula River basin have REE signatures similar to those of the Fort Payne Formation. Two different REE signatures were detected from Citronelle samples taken from the lower Pearl River basin. One signature

suggests that a portion of the Citronelle in the Pearl River valley may have come from west-central Tennessee, while the other signature suggests deposition from an upper Mississippi River source, but further research is needed to assess the exact origins of the Citronelle in the lower Pearl River valley. Based on these results, the hypothesis that the ancestral Tennessee crossed the state of Mississippi can be partially accepted. The Citronelle of the Pascagoula River basin contains cherts derived from the Fort Payne Formation of the southern Appalachians. This finding is similar to the results of the mineralogical analysis of Isphording (1983).

The phylogenetic analysis of *Doration* was inconclusive with respect to the course of the Tennessee River, but three trends regarding drainage patterns emerged. First, the *Doration* recovered as basal are endemic to drainages that flank the Nashville Dome which suggests that the breaching of the Fort Payne chert atop the dome in the Miocene (Luther, 1977; Stearns and Reesman, 1986; Reesman and Stearns, 1989; Galloway, 2005) acted as a vicariant event that led to their separation allowing them to evolve independent of one another. Second, a polytomy consisting of major tributaries to the Tombigbee River of the Mobile basin drainage and the Bear Creek system of the lower Tennessee River was consistently recovered across all loci sequenced from *Etheostoma stigmaeum*. This finding suggests that Bear Creek may have once been a tributary to the Tombigbee system. Wall (1968) hypothesized that a stream capture event may have occurred between Bear Creek and the Buttahatchee River of the Tombigbee system. Layman (1994), based on morphology and allozymes, also found that *Etheostoma stigmaeum* from Bear Creek and the Tombigbee were closely related, and the phylogenetic analyses support both Wall (1968) and Layman (1994). Finally, also consistently recovered across all loci is the monophyly of *Etheostoma stigmaeum* from the Pascagoula River system. When coupled with the results of the REE analysis, the monophyletic nature of *Etheostoma stigmaeum* in the Pascagoula River system suggests that the Pascagoula River may have a drainage history that is independent of that of its coastal plain neighbors (e.g., lower Pearl and Amite). It is possible that the course of the Pascagoula has been influenced either individually or by interactions of salt dome

mobilization in the Mississippi Salt basin that occurred as a result of differential loading of sediment along the domes as fluvial systems prograded across the coastal plain during lowstands, activity along the Pickens, Gilbertown, Quitman, and Pollard fault zones, and/or the Wiggins uplift (Ewing, 1991; Galloway et al., 1991). Also supporting the independence of the Pascagoula River basin is the presence of an undescribed endemic fish, *Fundulus* sp., in the basin (Slack et al., 2006).

The evolution of the Tennessee River is the result of complex interactions between geology and climate and determining the validity of hypotheses regarding its course is difficult due to its long history. Its long history increases the potential for historical drainage events to be superimposed upon one another and the erosion of sediments that could help recognize drainage events. Although geological evidence for the existence of an extra-basinal Tennessee River that crossed Mississippi exists, the geochemical and phylogenetic analyses employed neither support or refute its existence. With respect to the phylogenetic analyses, the results may be influenced by a lack of divergence time for *Etheostoma stigmaeum* in the drainages of the coastal plain. The results do, however, suggest that the stream capture events have occurred between the lower Tennessee and Tombigbee River systems, and that the Pascagoula River basin may have a history that is separate from other drainages on the coastal plain. More phylogenetic analyses of coastal plain taxa and the mapping of terraces along the coastal plain drainages may provide more insight into the history of both the Tennessee River and the coastal plain.

Oftentimes, the goals of phylogenetic analyses are to infer phylogenetic relationships and to recognize the presence of cryptic species. Secondary to these goals is the inference of biogeographic patterns. Rarely are phylogenetic analyses used to test drainage hypotheses, but when coupled with other forms of data such as geochemical and geomorphological analyses, they can reveal unrecognized patterns such as the independence of the Pascagoula River basin. Future investigations into the palaeodrainage history of the Tennessee River should employ all available lines of evidence.

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APPENDIX A

GEOLOGICAL MATERIALS EXAMINED

ID	Collecting Locality	Formation	Latitude/Longitude	
BP	Bayou Pierre streambed, Copiah County, MS	Citronelle Formation	31.8698N	-90.4988W
CS	Camp Shelby gravel quarry, Perry County, MS	Citronelle Formation	31.19765N	-89.10776W
MDH	Mad Dog Hill outcrop, Lawrence County, MS	Citronelle Formation	31.451346N	-90.071587W
TC	Topisaw Creek outcrop, Pike County, MS	Citronelle Formation	31.229179N	-90.282773W
BSPR	Blount Springs outcrop, Blount County, AL	Fort Payne Formation	33.928196N	-86.777427W
GC	Grinders Creek streambed, Lewis County, TN	Fort Payne Formation	35.463863N	-87.535418W
SRC	Standing Rock Creek outcrop, Stewart County, TN	Fort Payne Formation	36.44393N	-87.968938W
BC	Bear Creek bridge on HWY 17, Franklin County, AL	Tuscaloosa Formation	34.295787N	-87.803485W
LUX	Luxapalila Creek streambed, Lowndes County, MS	Tuscaloosa Formation	33.55984N	-88.31537W

APPENDIX B

COPY OF THE INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE (IACUC) APPROVAL FORM

THE UNIVERSITY OF SOUTHERN MISSISSIPPI

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE

118 College Drive #5147 | Hattiesburg, MS 39406-0001
Phone: 601.266.6820 | Fax: 601.266.5509 | betty.morgan@usm.edu | www.usm.edu/iacuc

INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.
PROTOCOL NUMBER: **10052401**
PROJECT TITLE: **Molecular Systematics of the Etheostoma subgenus Doration**
PROPOSED PROJECT DATES: **09/01/2009 to 08/31/2010**
PROJECT TYPE: **New Project**
PRINCIPAL INVESTIGATOR(S): **Mac Alford, Ph.D.**
College/Division: **College of Science & Technology**
DEPARTMENT: **Biological Sciences**
FUNDING AGENCY/SPONSOR: **N/A**
IACUC COMMITTEE ACTION: **Designated Reviewer Approval**
PROTOCOL EXPIRATION DATE: **09/30/2012**

Robert C. Bateman, Jr., Ph.D.
IACUC Chair

May 24, 2010
Date

APPENDIX C

ICHTHYOLOGICAL MATERIALS EXAMINED

Species & Field/Accession/Gen Bank Number (If Available)	Locality (If Available)
INGROUP	
Etheostoma akatulo	
YFTC 6571	Caney Fork, Warren County, TN
Etheostoma jessiae	
TVA 765-1	Betsy Willis Creek, Coffee County, TN
TVA 2888-3	Cypress Creek, Lauderdale County, AL
TVA 3571-1	East Fork Mulberry Creek Lincoln County, TN
TVA 5987-1	Knob Creek, Lawrence County, TN
TVA 9481	Big Sewee Creek, Meigs County, TN
TVA 11396-1	Tiger Creek, Catoosa County, GA
Etheostoma meadiae	
SLP 09-19	Clinch River, Hancock County, TN
Etheostoma stigmaeum	
AKP 07-1	Luxapalila Creek, Lowndes County, MS
AKP 07-3	Bowie Creek, Covington County, MS
AKP 08-2	East Fork Amite River, Amite County, MS
AKP 08-6	Noxubee River, Winston County, MS
AKP 09-2	Turkey Creek, Attala County, MS
AKP 10-3	Topisaw Creek, Pike County, MS
MMNS 361	Minter Creek, Greene County, AL
MMNS 394	Gravel Creek, Wilcox County, AL
MMNS 623	Strong River, Simpson County, MS
MMNS 835	Sucarnoochee River, Kemper County, MS
MMNS 889	Big Black River, Montgomery County, MS
MMNS 934	Yellow Creek, Lowndes County, MS
MMNS 967	Buttahatchee River, Monroe County, MS
MMNS 1000	Cahaba River, Bibb County, AL
MMNS 1077	Shutispear Creek, Calhoun County, MS
MMNS 1143	Bayou Pierre, Copiah County, MS
UAIC 13011.23	Bogueloosa Creek, Choctaw County, AL
UAIC 13489.05	Conasauga River, Polk County, TN
UAIC 15483.01	Black Warrior River, Tuscaloosa County, AL
UAIC 15489.01	Big Canoe Creek, St. Clair County, AL
USM	Homochitto River, Franklin County, MS
WTS 08-22	Bear Creek, Tishomingo County, MS
WTS 08-25	Bear Creek, Tishomingo County, MS

Species & Field/Accession/Gen Bank Number (If Available)	Locality (If Available)
E. sp. beaded darter	
YFTC 10732	Ouachita River, Montgomery County, AR
E. sp. bluegrass darter	
KYFWR	Green River, Green County, KY
E. sp. clown darter	
AKP 09-3	Grinders Creek, Lewis County, TN
TVA 3595-1	Flat Creek, Bedford County, TN
E. sp. highland darter	
USM 33689	Strawberry River, Sharp County, AR
E. sp. longhunt darter	
KYFWR	South Fork Rockcastle River, Jackson County, KY
OUTGROUP	
Crystallaria asprella	
GenBank AF045352.1	
Etheostoma chlorosoma	
MMNS 799	Homochitto River, Wilkinson County, MS
Etheostoma cinereum	
GenBank AY560360.1	
Etheostoma edwini	
GenBank AY374267.1	
Etheostoma flabellare	
GenBank AF045342.1	
Etheostoma gracile	
GenBank AF045345.1	
Etheostoma lynceum	
GenBank AY964716.1	
Etheostoma microperca	
GenBank FJ381003.1	
Etheostoma parvipinne	
GenBank AY374270.1	

Species & Field/Accession/Gen Bank Number (If Available)	Locality (If Available)
Etheostoma punctulatum GenBank FJ381007.1	
Etheostoma ramseyi MMNS 394	Gravel Creek, Wilcox County, AL
Etheostoma rubrum GenBank AF274446.1	
Etheostoma saggita GenBank AF045343.1	
Etheostoma simoterum GenBank AF288445.1	
Etheostoma spectabile GenBank AF045344.1	
Perca fluviatilis GenBank AF045358.1	
Percina roanoka GenBank AF386597.1	
Percina sciera GenBank AF386574.1	
Romanichthys valsanicola GenBank AF045361.1	
Sander lucioperca GenBank GU936790.1	
Zingel zingel GenBank AF546124.1	

Abbreviations are as follows: AKP – field notes of Andrea Karen Persons, MMNS – Mississippi Musuem of Natural Science, UAIC – University of Alabama Ichthyological Collection, WTS – field notes of William Todd Slack, TVA – Tennessee Valley Authority, KYFWR – Kentucky Fish and Wildlife Resources, USM – University of Southern Mississippi, SLP – field notes of Steven L. Powers, and YFTC – Yale Fish Tissue Collection.